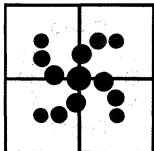


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AGRICULTURE

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Contributions toward  
a Reclassification  
of the Formicidae.  
V. Ponerinae,  
Tribes Platythyreini,  
Cerapachyini,  
Cylindromyrmecini,  
Acanthostichini,  
and Aenictogitini

by William L. Brown, Jr.

*annotation copy.*

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# Contributions toward a Reclassification of the Formicidae. V. Ponerinae, Tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini

William L. Brown, Jr.\*

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## INTRODUCTION

Previous parts of this reclassification have dealt with Platythyreini (Part I, Brown 1952), Ectatommini (Part II, Brown 1958), Amblyoponini (Part III, Brown 1960), and Typhlomymecini (Part IV, Brown 1965).

The present format of the series, which for each part included generic diagnoses and species lists, plus keys to species wherever practicable, and also an Appendix for new species, discussion of synonymy, biological notes, and similar information, began only with Part II. For that reason, I have redone the Platythyreini in the more complete format and have included the treatment here, together with that of the genera placed in subfamily Cerapachyinae at one time or another. The cerapachyines are here considered as 3 separate tribes within subfamily Ponerinae: Cerapachyini, Cylindromyrmecini, and Acanthostichini.

Aenictogitini, containing the sole genus *Aenictogiton*, known only from a few males taken at light in equatorial Africa, is dealt with in this section as a matter of arbitrary convenience. Its affinities are unknown, and it is included only provisionally among the Ponerinae.

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## SOURCES OF MATERIAL

By far the most important depository of specimens used in this study is in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, here

abbreviated MCZ. The ant collection is based on the lifetime accumulation of W. M. Wheeler and his students, particularly W. M. Mann and N. A. Weber, but since 1948 it has trebled in size to about 500 Cornell-type drawers of specimens. The increment is due partly to the accession of the collections of B. Finzi, J. W. Chapman, and N. A. Weber, but even more significantly to the greatly increased rate of field collecting trips, beginning in 1950, supported mainly by agencies of Harvard University and the (U.S.) National Science Foundation.

In particular, E. O. Wilson and I have been enabled to sample the formicid faunas over a wide and fairly representative spread of the earth's ant-inhabited countries, and to gather the ants as they should be gathered—in clean, strong colony-series, with larvae and often with queens and males—and accompanied by data on habitat, behavior, and ecological role.

Even though our generation can claim more than a modest gain in this kind of information over what our surface-bound predecessors accomplished, our experience teaches us that we have only begun to find out what the ants of the whole world are, let alone what they do. And what ants do, especially in warm deserts and tropical forests, is increasingly recognized as important on the grand ecological scale.

Beyond MCZ, repositories fall into two main classes: the collections of the classical European myrmecologists, the first seven listed below, and other collections, pre-

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dominantly of a later date, in Europe and elsewhere.

- British Museum (Natural History), London, England (BMNH-London). Collections of F. Smith, W. C. Crawley, H. St. J. K. Donisthorpe, and others. The British Museum has also had on loan types of Smith and Crawley from the Hope Department of Entomology of Oxford University.
- Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy (MCSN-Genoa). Collection of Carlo Emery.
- Muséum d'Histoire Naturelle, Geneva, Switzerland (MHN-Genève). Collection of A. Forêt.
- Muséum Nationale d'Histoire Naturelle, Paris, France (MNHN-Paris). Collections of Ernest André and others.
- Museum für Naturkunde an der Humboldt Universität zu Berlin (MNK-Berlin). Collections of Roger, Stütz, and Viehmeier.
- Naturhistorisches Museum, Basel, Switzerland (NM-Basel). Collection of F. Santschi.
- Naturhistorisches Museum, Vienna, Austria (NM-Vienna). Collection of G. Mayr.
- American Museum of Natural History, New York City, U.S.A. (AMNH-NY). Parts of collections of W. M. Wheeler, N. A. Weber, and others.
- Australian National Insect Collection, Canberra, Australia (ANIC-Canberra). This collection is currently maintained by the Commonwealth Scientific and Industrial Research Organization of the Australian Commonwealth Government. It contains part of the material of John Clark and more recent additions by R. W. Taylor and T. Greaves.
- California Academy of Sciences, San Francisco, U.S.A. (CAS-San Francisco). The important material here is mainly that gathered by E. S. Ross and his colleagues on worldwide excursions.
- United States National Museum of Natural History, Washington, D. C., U.S.A. (USNM-Washington). Collections of M. R. Smith, part of that of W. M. Mann, and others.
- Universitets Zoologiske Museum, Copenhagen, Denmark (UZM-Copenhagen). Contains type material of various authors, particularly of Forêt.
- Walter W. Kempf Collection, including the ant collections of T. Borgmeier, São Paulo, Brasil (WWK). This collection is kept in the City of São Paulo at present writing, but may soon be moved to Brasília.

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I owe special thanks to colleagues abroad who helped in more than ordinary ways to further the success of my collecting trips: Dr. Paulo Vanzolini, Director of the Museu de Zoologia, Universidade de São Paulo; Messrs. Graham Guy and Don Broadley, of the National Museums of Rhodesia, and Charles Jacot-Guillarmod and Laurie Weatherill, of the Albany Museum, Grahamstown, South Africa; Dr. Sampurno Kadaras, Director, Museum Zoologicum, Bogor, Indonesia; and Drs. A. Benedict Soans and Joyce Soans, of the Malabar Christian College, Calicut, Kerala State, India.

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#### SPECIES LISTS AND TERMINOLOGY

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In this part of the reclassification, I have followed the practice of Parts II (Brown, 1958) and III (Brown, 1960) in listing all the species in each genus. I have improved the listing somewhat by entering under each genus all the species (subspecies, varieties) originally described in that genus, and all that I consider to belong there now. In case a species has been transferred to another genus, the situation is indicated by the word "to", followed by the name of the genus in which the species is now placed. For example, under *Cerapachys*, *femoralis* Motschulsky is followed by "to *Tetraponera*", meaning that this species has been transferred from *Cerapachys* to *Tetraponera*.

The capital letters placed in parentheses before each specific name indicate the kind of evidence upon which the present generic placement is directly based.

(T) indicates that type material, nidotypes, reliably type-compared material, or similarly authentic specimens have been examined, in most cases by myself; rarely, examination has been made by other myrmecologists.

(P) means that material identified from reasonably good descriptions or other satisfactory evidence has been examined and is thought to be correctly determined.

In cases where the species is not seriously questioned, but no specimens referable to it have been seen, or, if seen, cannot be satisfactorily verified as to identity, no entry has been made before the species name.

(?) signifies that, in my opinion, the species is inadequately described for purposes of distinction and that its taxonomic status is doubtful.

Measurements and indices and their abbreviations used in the keys, and in the descriptions in the Appendix, are those now virtually standard in ant taxonomy. In general, L means "maximum measurable length", and W, "maximum width". TL, for total length of body, is the summed length of head with closed mandibles, diagonal length of trunk, and axial length of petiole and the remainder of the abdominal (postpetiolar and gastric) segments. HL is head length measured in dorsal full-face view, that is, perpendicularly to the main axis of the cranium; the measurement is difficult to take in many of the species in the genera discussed here, especially *Cerapachyini*, in which the anterior and posterior borders of the head may change shape radically as it is tilted even slightly forward or backward. Sometimes, in order to reflect better the actual shape of the main part of the cranium, HL is taken from the anterolateral corners of the head, ignoring projecting parts of the clypeus or frontal carinae, but in this case, the circumstances are always cited with the mea-

surement. HW is also taken in full-face view, and unless otherwise stated, excludes the compound eyes. Measurements "across" the eyes are meant to include them in HW; in most of the species dealt with here, HW is maximal a little behind the eyes. ML, length of closed mandibles, is taken while head is viewed full face, and consequently gives a foreshortened value for the more or less downturned mandibles, which are rather short in all the groups here covered, except in some platythreine species.

Scape L excludes the narrowed basal neck of the scape. Greatest diameter of eye is taken from the inner edge of the circumocular groove, if present, and in any case is meant to include all the ommatidia, pigmented or not. WL, or Weber's length of trunk, is taken in side view diagonally from the anterior descending face or edge of the pronotum (cervix excluded) to the most posterior point of the trunk—usually either the inferior propodeal plate on the side toward the observer, or the median extremity of the propodeum. Measurements of petiolar node and postpetiole are taken from directly above these segments, and normally exclude anterior or posterior peduncles, if these are present. The only index frequently used in this part is CI, or cephalic index, which is  $HW \times 100 / HL$ , a quantity that is more than usually variable in many species dealt with here because of the special difficulty in getting consistent values of HL.

Some anatomical terms require brief comment here. I now use *trunk* (or, more formally, *truncus*) for *alitrunk*, equal to the fused *thorax + propodeum* in clistogastran Hymenoptera, in which the "waist" constriction comes between the first and second true abdominal somites. The old term "thorax" in myrmecology ignored the confusion generated, particularly in teaching, when this tagma was stretched to include the first abdominal somite. A newer term, *mesosoma*, is an unnecessarily proposed synonym of *alitrunk*, and has the serious disadvantage that it is used in different senses in arachnid morphology and taxonomy, and (as *mesosome*) in the genitalic nomenclature of mosquitoes and other nematoceran Diptera. *Alitrunk* is an old term, sanctioned in use for the higher Hymenoptera by such authors as R. J. Tillyard and V. S. L. Pate, and though it is not completely free of ambiguity in some older definitions, myrmecologists seem to have understood it well. The shortened version, *trunk* or *truncus*, seems to me even more advantageous, through its instantly recognizable functional analogy to the vertebrate trunk, in insects that so frequently lack the wings to justify *alitrunk*.

Some myrmecologists still use the term *epinotum*, introduced by Carlo Emery to replace the old "median segment" (true abdominal segment I), although Emery's term has been used almost exclusively for ants, while most other hymenopterists have long called the homologous segment *propodeum*. There seems to be no excuse for continuing *epinotum* as a special term just for ants. *Propodeum* (pro + pōdeon, Greek equivalent) is an elegantly descriptive

term. It indicates the part of an ant, wasp, or bee immediately before the "foot", that is, the petiole or neck of the abdominal "flask" or bottle. The "foot" (*pod-*) goes back to the days when wineskins were more prevalent than now in the Mediterranean countries, and a leg of the skin, then as now, formed the spout, the equivalent of a bottle's neck.

*Pedicel* as used in this work refers to the second segment of the antenna, following the basal segment or *scape*. This usage is in accord with that of general insectan morphology. *Funiculus* refers collectively to all the segments distal to the scape in ants; this usage varies from that in some other hymenopteran groups. The modified segments II and III of the true abdomen in these ants, called here *petiole* and *postpetiole*, are collectively the *waist* (not *pedicel*, an old and confusing usage).

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## THE TRIBES

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### TRIBE PLATYTHYREINI

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Since 1952, our concept of platythyreine generic classification has changed, and advances have been registered also at the species level, so a new section on the Platythyreini is offered here to bring this early part of the reclassification into line with the developing format of the work.

In 1952, I recognized 4 genera of Platythyreini:

*Platythyrea*  
*Eubothroponera*  
*Probolomyrmex*  
*Escherichia*

My suspicion that *Escherichia* was a synonym of *Probolomyrmex* has been confirmed by Taylor (1965) in his revision of the latter genus, and I have been able to check this point myself in the Forel Collection (unpublished notes). Meanwhile, my study of adults and the study of the larvae by G. C. and J. Wheeler (1971) have tended to bridge the differences by which *Platythyrea* and *Eubothroponera* have been thought to be distinguished. It does not now seem possible to regard the species of *Eubothroponera* as more than a primitive, endemic, Australian species-group of *Platythyrea*. After the required synonymy, tribe Platythyreini contains just 2 distinct genera: *Platythyrea* and *Probolomyrmex*.

The treatment here is limited to a brief diagnosis and discussion of the genera, with species lists, regional keys, and revisions of some species-level situations. Species taxonomy of *Platythyrea* is more than usually difficult, and the revisions offered here need to be followed up. Taylor's (1965) revision of *Probolomyrmex* is the key work on the genus; my summary is taken in large part from that paper, with the addition of 2 new species and a few records.

## DIAGNOSIS

**Worker and queen:** Typical Ponerinae with elongate body and well-developed exsertile sting. Head slightly to markedly longer than broad, with sides parallel or gently converging in front. Compound eyes large, moderate in size, or absent. Ocelli always absent in worker, and sometimes even in winged queens. Antennae 12-segmented, with relatively long scape; funiculus very smooth in outline (without constrictions between segments), without a defined club, but sometimes gradually thickened apicad. Mandibles unremarkable, triangular or short and curved-horizontal, serially toothed, denticulate or edentate. Maxillary palpi with 3-6 segments, labial palpi with 2-4 segments.

Promesonotal suture present and apparently flexible (*Platythyrea*) or absent (*Probolomyrmex*); other sutures or grooves on truncal dorsum indistinct or lacking. Propodeal angles variably armed with sharp or blunt margins, or even blunt, tooth-like processes; the declivity concave from side to side, and often from top to bottom as well. Petiole sessile, node more or less rounded anterodorsally, but with a usually truncate, excavate, or at least abruptly descending posterior face; posterodorsal border usually (but not always) marginate, or with 2 or 3 teeth or low, angular or rounded processes. Subpetiolar process present in some form. Gaster long-cylindrical, with a tapered apex; postpetiolar (third true abdominal) segment much larger than petiole and subequal to the succeeding segment, and therefore an integral part of the gaster, although it is separated from the rest of the gaster by a modest constriction, at least in side view. Stridulatory file present on the pretergite of the second gastric segment in *Platythyrea* but lacking in *Probolomyrmex*.

Legs with at least one pectinate spur on each tibial apex; tarsal claws with or without a submedian tooth.

Sculpture and pilosity fine, usually reduced to an opaque or subopaque pruinose condition that is particularly characteristic, with erect pilosity restricted at most to mandibles, clypeus, gastric apex, and the meatus of the metapleural gland; but in a few (*Platythyrea*) species, short, fine, erect or suberect hairs are on the body and appendage surfaces and may be rather abundant. The sculpture apparently consists of extremely fine, dense punctation, often too small to be resolved at magnification upwards of 100× with the light microscope, and associated with this is often a more or less well-developed, but never obtrusive, fine, short, appressed pubescence. In addition, a coarser but still rather shallow sprinkling of larger round punctures or foveolae is superimposed on the fine pruinose integument; this coarser punctation is probably always present in some form, but is variably distinct in different parts of the body and in different species, and varies also in gauge and density.

Color ranging from ferruginous to black, sometimes with contrasting yellowish or reddish antennae and legs,

but, even in the black species, the callow period seems to last a long time as far as pigmentation is concerned, and yellow, reddish, or brown forms of normally black species are common.

The reader may have noted that the important characters of antennal insertions, clypeal form, and frontal lobes and carinae were not mentioned in the preceding remarks. These structures differ strikingly in the 2 genera of *Platythyreini*, *Platythyrea* and *Probolomyrmex*, and it seems foolish to make a tribal definition that contains such wide differences as these or, for example, those in wing venation or larval form.

**Male:** Typically proponerine in form, differing rather modestly from the queens in size and other characters, as compared with the higher subfamilies or even in tribe Ponerini. Mandibles opposable or crossing over at full closure. Head broader than long, with much larger, more convex eyes than in workers. Antennae 13-merous, smooth. Genitalia retractile; pygidium sometimes terminating in a point or in a downcurved spine like that of many Ponerini males. Genitalia including recognizable parameres, laciniae, and aedeagus, the last generally with at least some serration on the ventral edge.

**DISTRIBUTION:** Mainly tropical, with limited extensions into subtropical regions on all main continents, New Guinea, and Madagascar.

**BIONOMICS:** *Platythyrea* is known only from scattered observations. Most of the species are known from stray workers or small colonies in rotten wood, or from beetle burrows, hollow twigs, and similar cavities in standing live or fallen dead trees. Many of the species can be found on logs or tree trunks at forest edges in the tropics, running very rapidly over bark or leaves of trees. I have found *P. sinuata* running with marvellous speed and grace over leaves in living tree foliage more than 15 meters above the ground, and several of the African and Indo-Australian species are so agile that they are extremely difficult to catch. The large African species — *P. cribrinodis*, *P. lamellosa*, *P. arnoldi*, and *P. schultzei* — are ground dwellers and forage on the ground or on trees and shrubs. I found *P. cribrinodis* nesting in the bases of large earthen termitaries in Rhodesia, and also in grassland under large stones.

Termites seem to make up a large part of the diet of a number of *Platythyrea* species the world around, but Arnold (1915:29) found that *P. arnoldi* in Rhodesia feeds entirely on adult beetles, especially Tenebrionidae.

The sting of *Platythyrea* is more severe, in my experience, than that of most ponerines, size for size. A sting of *P. sinuata* (in Panama) on my hand caused a deep throbbing pain that lasted most of one day, and left lingering tenderness for another day. Even the little *P. parallela* has a lasting sting to be respected, and I would expect that of the larger African species to be very painful, though I have not experienced it.

There is not much information about nesting, food, or

foraging of *Probolomyrmex*, but the species all appear to be rare and relatively cryptic (or nocturnal?) in foraging habits. Species have been collected mainly in forest litter or soil, usually in the tropics, and they nest in hollow twigs, burrows, or small pieces of rotten wood in or on the soil. Their food is unknown.

**RELATIONSHIPS:** It is certainly hard to escape the impression that the *Platythyreini* are related to the Ponerini. Not only is the habitus in general similar in all three castes of the more primitive members of each tribe, but there are also particular characters, for example, the downcurved pygidial spine shared by the males of many species in both tribes and the detailed correspondence of the primitive wing venations, which do not seem readily ascribable to convergent evolution. Even the best, general, differential worker-queen character — the structure of the clypeus, frontal area and frontal carinae — is a matter of degree rather than a clear-cut distinction. Nevertheless, the *Platythyreini* have two primitive characters that mark them as closer to the basic stock of the Ponerinae than are the Ponerini:

1. The male mandibles in *Platythyreini*, so far as known, are triangular and opposable, or cross over each other at full closure, while in Ponerini they are always reduced and nonopposable.

2. Some worker-queen *Platythyrea* still possess the primitive formicid palpal segmentation of 6 maxillary, 4 labial palpomeres. The highest count in worker-queen Ponerini is only 4,4, so that 2 segments of the maxillary palpi have been lost in females of the latter tribe. Quite a few male Ponerini still carry the 6,4 palpi.

The larvae of *Platythyreini* are somewhat ambiguous, especially since Taylor (1965:348) described the cast cuticle of the last-instar larva of *Probolomyrmex angusticeps*. This larva has low mammiform tubercles in rows on the body segments, but these tubercles are not especially like those of Ponerini, and there are no substantial hairs on the head or body. Owing to the nature of the material, we do not know exactly what the larval body shape is. However, if Taylor's figures 3 and 4 represent this accurately (he did observe living larvae in addition to the cuticles figured), it is quite different from the *Platythyrea* shape by being straight, tapered at both ends, and without a slender "neck" in the thoracic region. Like *Platythyrea*, the last somite does form a bluntly rounded, ventrally projecting "tail", but in *Probolomyrmex*, the last somite also bears, on the dorsal side near its base, a prominent, stalked "sensory process," resembling a rubber sucker-disc, by means of which the larvae are attached to the ceiling or walls of the nest chamber.

The known larvae of *Platythyrea* (G. C. and J. Wheeler, 1952, 1971:1198) are much more "proponerine" in appearance (G. C. and J. Wheeler, 1964:459). They are non-tuberculate, unless some irregular papillae and small welts on the ventral surface be counted as tubercles, and much

of the cuticular surface is densely spinulose and covered with short, simple to short-multifid hairs. The body is stout, but the thoracic and first abdominal somites are drawn out into a slender neck, curving ventrad, much as in the Wheeler's generalized ectatommiiform or pachycondyliiform body shape. The mandibles (G. C. and J. Wheeler, 1964:459, fig. 17, D1) are narrowly subtriangular, the thin mesial blade with a few fine irregular denticles, or 2 preapical teeth and some denticles, in addition to the acute, mesially curved apex. In *Probolomyrmex*, the mandibles are still narrower and straighter in frontal view, and there are 2 minute preapical teeth on the mesial margin. The primitive larval mandible in Ponerinae (and in Formicidae) has 3 strong teeth, an apical and 2 preapicals, so that the larval mandibles of *Platythyrea* and *Probolomyrmex* must both be considered as slightly modified (derived) from the primitive condition. The *Platythyrea* larva is more primitive generally and fits the proponerine pattern, despite the relatively minor divergences in mandibular form and in the presence of small ventral processes and welts. I guess that the *Probolomyrmex* larva is derived from the *Platythyrea* type, and that the tubercles of the former evolved by convergence with those of larvae of tribe Ponerini. Still, *Platythyreini* and *Ponerini* are probably so closely related that we should not rule out all possibility that the tubercles of *Ponerini* and *Probolomyrmex* were derived from a common ancestor with tuberculate larvae. If this were the case, the ventral papillae and welts of *Platythyrea* larvae just might be the vestiges of a more complete ancestral pattern of tuberculation.

In other adult female ponerine characters, such as toothed tarsal claws, bicalcarate mid- and hind-tibial apices, full venation of both sets of wings, and the presence of an anal lobe on the hind wing, both *Platythyreini* and *Ponerini* have many species that qualify across the board as primitive. In the male genital capsule, all the structures can be matched as homologous in *Platythyreini* and *Ponerini*, as well as the known species of the other tribes of Ponerinae.

The *Platythyreini* have followed a different course of evolution from the *Ectatommini*, yet the more primitive members of these two tribes share fundamental similarities,

such as larval form and pilosity, male mandible type, and the female palpal formula of 6, 4, plus the characters mentioned in the preceding paragraph. No single ectatommine species carries all of these primitive character states at once, however, and one has to postulate an archetypal ectatommine that combines all the traits needed to produce something as completely primitive as certain *Platythyrea* species appear to be. Only in the more complete division of the worker trunk by sutures do some ectatommines (e.g. *Ectatomma*) have a character more primitive than in any *Platythyreine*. From these considerations, it seems that *Ectatommini* and *Platythyreini* are cognate tribes in the "Proponerinae," and that *Ponerini* (including *Odontomachini* and possibly *Thaumatomyrmex*) represent a line even more closely cognate with the *Platythyreini*. All 3 tribes go back to Baltic Amber times, and no doubt to even earlier in the Tertiary or beyond. *Ectatommini* represents an old, dominant lineage that spread world wide early; it is being replaced from the Afro-Asian heartland outward by *Ponerini*. *Platythyreini* is the old, slowly dwindling sister-group of the *Ponerini*, specialized in different ways in different zoogeographical realms, but nowhere threatening dominance.

## Platythyrea

- > *Platythyrea* Roger, 1863, Berlin. Entomol. Zeitschr., 7:172, ♀. Type: *Platythyrea punctata* (F. Smith), by designation of Bingham, 1903.
- > *Platythyrea*: Emery, 1911:28-30, pl. 2, fig. 1, lb, ♂ ♀ ♂ diagnoses, species list.—Wheeler, 1922a:57-60, diagnosis; 1922c:758-761, list of African spp.; 1922d:1007, list of Malagasy spp.—Wilson, 1958b:150-153, revision of Melanesian spp.—Kempf, 1972:206, neotropical species list.
- ≈ *Ponera*: F. Smith, 1858:95.—Gerstaecker, 1859:262.—Roger, 1860:295.
- ≈ *Pachycondyla* F. Smith, 1858:95.
- ≈ *Pachycondyla* subgenus *Bothroponera*: Forel, 1913b:176.
- > *Eubothroponera* Clark, 1930:8-9, ♀. Type: *Eubothroponera dentinodis* Clark, by original designation.—Clark, 1934a:32-34; designation of *E. tasmaniensis* as type invalid.—Clark, 1938:361.—Brown, 1952:2-5, transfer to *Platythyreini*, discussion. New synonymy.

A diagnosis is given here in side-by-side comparison with that of *Probolomyrmex*.

## PLATYTHYREA

**Worker:** Size modest to large; TL 4 to about 20 mm.

Antennal insertions remote and roofed by broad horizontal frontal lobes, situated behind clypeus and away from (behind) anterior border of head. Clypeus broad, with lateral wings, nearly flat to strongly convex, with or without a depressed narrow anterior apron. Posterior margin of clypeus varying from fine but distinct, to indistinct, or even absent, so that the surfaces of the posterior clypeus, frontal triangle, and frontal lobes tend to be confluent. Frontal triangle at most weakly impressed, with or without a shallow trailing median sulcus separating the frontal lobes.

Mandibles prominent, exposed, triangular, with distinct masticatory and basal borders, the blades extended but more or less downcurved; masticatory border serially dentate or denticulate, or edentate and cultrate; basidorsal surface with or without an oblique groove running lateroapical to the outer margin. Palpal formula 6, 4 to 3, 2.

Compound eyes always present and multifaceted, modest to large in size, situated near or in front of middle of sides of the head.

Antennal scapes reaching very nearly to or (usually) beyond posterior border of head in full-face view.

Trunk with a complete and apparently flexible pronotal suture.

Middle and hind tibiae each with 2 (large mesal, smaller lateral) pectinate spurs; tarsal claws usually each with a distinct or indistinct median tooth.

Full adult color ranging from deep yellowish brown to black, the appendages often a contrasting lighter hue.

**Queen:** Much like corresponding worker in size and form, but winged as virgin and with moderately well-developed pterothoracic sclerites. Notauli absent or weak and incomplete. Ocelli present, weak, or even entirely absent; the last a condition otherwise unknown among winged queen ants. Venation complete for ants in both fore and hind wings; anal lobe present in hind wing.

**Male:** Size nearly that of corresponding workers and queens.

Head broader than long, including large compound eyes (fig. 32). Mandibles triangular, exposed, opposable. Antennal insertions remote and positioned behind a broad, convex clypeus.

Notauli present, usually strong and complete; parapsidal furrows present, fine. Metanotum variable, sometimes with a blunt point. Wings as in queen. Middle and hind legs with bicalcarate tibial apices, tarsal claws each with a median tooth so far as known.

Petiolar node more or less like that of corresponding worker and queen, though posterodorsal margination, teeth, etc. generally less distinct in the males so far known.

Genital capsule retractile, with all primitive parts present and well developed (figs. 131-136). Pygidium distinctive, usually tapered toward apex and sometimes produced as a downcurved aculeus. Cerci present and normally exposed (fig. 135).

## PROBOLOMYRMEX

**Worker:** Size small; TL only 2.4-4.2 mm.

Antennal insertions very close together and situated far forward on a platelike extension of the anterior part of the head, consisting of the shortened clypeus fused with the surrounds of the antennal insertions and the completely eclipsed frontal area. Separating the antennal insertions is a thin, rounded vertical plate representing the raised and fused frontal lobes. The clypeo-frontal structure covers the small curved mandibles, which are modified-triangular, each with a short masticatory border carrying an acute apical tooth and a few small, serially crowded teeth or denticles basad. No basidorsal mandibular groove. Palpal formula, so far as known, 4, 2.

Compound eyes usually absent in worker; present and rather small in one species, and even in this case, the specimen could be an ergatoid queen. Ocelli absent.

Antennal scapes fail to reach posterior border of head by a considerable margin.

Trunk completely fused into one structure; without dorsal sutures.

Middle and hind tibiae each with a single spur; tarsal claws simple.

Full adult color yellowish brown to red brown.

**Queen:** Much like worker in size and form, but winged when virgin. Ocelli present and fairly well developed. Flight sclerites developed. Venation greatly reduced; in fore wing, consisting only of R+Sc, Stigma, M+CuA, and basal vein (with closed CuA continuing free to hind margin) forming a single closed ("median") cell, and a floating radiapex (=2r continued into the apical free abscissa of Rs, which does not reach margin). In the narrow hind wing, only a single vein persists (R) in the basal half of the wing near the anterior margin, and there are 3 submedian hamuli; anal lobe absent. Compound eyes moderately well developed.

Color as in worker.

**Male:** Size nearly that of corresponding workers and queens.

Head subglobose, including large eyes, slightly broader than long. Mandibles short, subtriangular, opposable, mostly covered by the projecting clypeofrontal plate with its fused vertical frontal lobes. Antennal insertions on the clypeofrontal plate, at the very anterior margin of the head. The plate itself is not as strongly projecting as in the workers and queens.

Notauli lacking. Metanotum forms a blunt median tooth. Wings as in queen. Middle and hind legs each with a single tibial spur. Tarsal claws simple.

Petiolar node rounded above, and rounded into posterior face without margin, teeth, or angles.

Genitalia, according to Taylor, with all primitive parts. Pygidium with rounded apex. Cerci absent (or vestigial?).

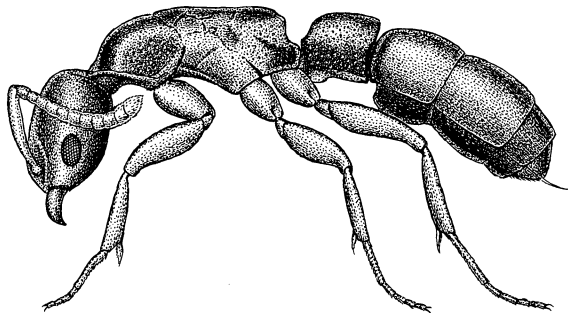


Figure 1. *Platythyrea parallela*, side view of worker (after Wilson and Taylor).

# **PLATYTHYREA species**

## (\*New combinations formerly in *Eubothroponera*.)

- angusta* Forel 1901:336 ♀ Amazon-Orinoco Basins; Trinidad [17]
- (T) *annamita* Forel = *parallela*
- (P) *apicalis* Santschi = *arnoldi*
- (T) *arnoldi* Forel 1913:206 ♀ C & E Africa [8]
- = *apicalis* Santschi 1937:71 ♀ n. syn.
- arthuri* Forel 1910:15 ♂ Madagascar
- arwana* Karawajew = *parallela*
- (T) *australis* Forel = *parallela*
- (T) *bequaerti* Forel = *schultzei*
- (T) *bicolor* (Clark) \* = *turneri*
- (T) *bidentata* Brown n. sp. ♀ Philippines [13]
- (T) *bicuspid* Emery 1900:268 ♂ Madagascar [15]
- boliviana* Santschi = *simata*
- (P) *brevidentata* Wheeler = *cribrinodis*
- (T) *brevinodis* Santschi = *cribrinodis*
- (?) *brunneipes* (Clark) \* 1938:361 ♀ S Australia; Reevesby I. [16]
- (T) *cephalotes* Viehmeyer = *parallela*
- (T) *ceylonensis* Donisthorpe = *parallela*
- cinnerea* Forel = *punctata*
- (T) *clypeata* Forel 1911:378 ♀ SE Asia [13]
- = *thwaitesi* Donisthorpe 1931:496 ♀ n. syn.
- (T) *conradi* Emery 1899:464 ♂ W & C Africa [7]
- = *monodi* Bernard 1952:185 ♀ n. syn.
- (T) *cooperi* Arnold 1915:29 ♂ S Africa; Natal
- (T) *coxalis* Emery = *parallela*
- (P) *cribrinodis* (Gerstaecker) 1858:262 ♀ E Africa *palpi 3, 2*
- = *brevinodis* Santschi 1914:47 ♀ n. syn.
- = *punctata* Arnold 1915:24 ♀ preoccupied, n. syn.
- = *brevidentata* Wheeler 1922:759, nom. pro *punctata* Arnold, n. syn.
- (T) *crucheti* Santschi 1911:205 ♀ Angola [7]
- (T) *cylindrica* Forel = *parallela*
- (T) *cyrtulii* Forel = *schultzei*
- (T) *debilis* Forel = *mocquerysi*
- (T) *dentinodis* (Clark) 1930:9 ♀ SW Australia [16]

- (T) *egena* Viehmeyer = *parallela*
- (T) *exigua* Kempf 1964:142 ♀ ♀ N Mato Grosso [17]
- (T) *frontalis* Emery 1899:466 ♀ ♀ W, C, E Africa [4]
- (T) *gracillens* Santschi = *gracillima*
- (T) *gracillima* Wheeler 1922:59 ♀ C & W Africa [13]
- = *gracillens* Santschi 1937:73, variant spelling of *gracillima*
- (T) *grisea* (Forel) = *lamellosa*
- (T) *incerta* Emery = *pilosula*
- (T) *inconspicua* Mayr = *parallela*
- (P) *inermis* Forel 1910:122 ♀ Philippines [12]
- = *maquilingi* Wheeler & Chapman 1925:58 ♀ n. syn.
- (T) *javana* Forel = *parallela*
- (P) *lamellosa* (Roger) 1860:295 ♀ C & S Africa [8]
- = *longinoda* Forel 1894:75 ♀ n. syn.
- = *suturalis* Forel 1901:64 ♀ n. syn.
- = *grisea* (Forel) 1910:5 ♂ syn. Wheeler 1922:760
- = *rhodesiana* Forel 1913:110 ♂ ♂ n. syn.
- (T) *lata* Santschi = *schultzei*
- (T) *longinoda* Forel = *lamellosa*
- (T) *maquilingi* Wheeler & Chapman = *inermis*
- (?) *matapoensis* Arnold, 1915:32, "queen" (recte worker?) [2]
- (T) *meineri* Forel = *simata*
- (T) *micans* (Clark) \* 1930:10 ♀ SW Australia [16]
- (T) *mocquerysi* Emery 1900:270 ♀ ♀ Madagascar [3]
- = *debilis* Forel 1907:76 ♀ n. syn.
- (T) *modesta* Emery 1899:467 ♀ W & C Africa [2]
- (T) *monodi* Bernard = *conradi*
- (T) *nicobarensis* Forel 1905:165 ♀ Nicobar Is.; Nancovri [10]
- occidentalis* André 1890:315 ♀ W & C Africa [6]
- (T) *pacifici* Santschi = *parallela*
- (T) *parallela* (F. Smith) 1859:143 ♀ Indo-Australian tropical region; Seychelles [9]
- = *inconspicua* Mayr, 1870:961 ♀ n. syn.
- = *pavula* Emery 1893:188 ♀ syn. Wilson 1958:150
- = *coxalis* Emery 1893:189 ♀ syn. Wilson 1958:150
- = *urugthonii* Forel 1900:315 ♀ (?) n. syn.
- = *victoriae* Forel 1900:316 ♀ n. syn.

- = *subtilis* Emery 1901:666 ♀ n. syn.  
 = *tritschleri* Forel 1901:338 ♀ n. syn.  
 = *javana* Forel 1905:5 ♀ ♀ n. syn.  
 = *annamita* Forel 1911:215 ♀ n. syn.  
 = *sechellensis* Forel 1912:159 ♀ n. syn.  
 = *cylindrica* Forel 1913:5 ♀ n. syn.  
 = *australis* Forel 1915:10 ♀ n. syn.  
 = *parva* Crawley 1915:133 ♀ n. syn.  
 = *egena* Viehmeyer 1916:111 ♀ ♀ n. syn.  
 = *philippinus* Viehmeyer 1916:283 ♀ n. syn.  
 = *cephalotes* Viehmeyer 1924:224 ♀ n. syn.  
 = *arana* Karavaiev 1925:75 ♀ prov. syn. of Wilson 1958:150 (confirmed)  
 = *pulchella* Santschi 1928:121 ♀ n. syn.  
 = *pacific* Santschi 1928:43 ♀ n. syn. Wilson & Taylor 1967:20  
 = *ceylonensis* Donisthorpe 1941:202 ♀ ♀ n. syn.  
 (T) *parva* Crawley = *parallela*  
 (T) *penangensis* Wheeler = *tricuspidata*  
 (T) *philippinus* Viehmeyer = *parallela*  
 (T) *pitulula* (F. Smith) 1858:93 ♀ tropical S. America [17]  
 = *incerta* Emery 1890:56 ♀ n. syn.  
 (T) *primava* Wheeler 1914:36 ♀, ergatoid, Baltic Amber  
 (T) *pruinosa* Mayr = *punctata*  
 (T) *pulchella* Santschi = *parallela*  
 (T) *punctata* (F. Smith) 1858:108 ♂ ♂ Florida; Mexico; W. Indies; C. America [17]  
 = *pruinosa* Mayr 1870:962 ♀  
 = *cineracea* Forel 1886:39 ♀  
 (P) *punctata* Arnold = *cribrinodis*  
 (T) *pusilla* Emery = *parallela*  
 (T) *quadridenta* Donisthorpe 1941:134 ♀ New Guinea; Borneo [14]  
 (T) *recta* Santschi = *schultzei*  
 (T) *reticulata* (Clark) \* = *turneri*  
 (T) *rhodesiana* Forel = *lamellosa*  
*ruficornis* (Spinola) 1851 *nomen dubium et oblitum* Emery 1911:28  
 (T) *sagei* Forel 1900:315 ♀ India [14]  
 (T) *schultzei* Forel 1910:3 ♀ E, C, & S Africa [5]  
 = *bequaerti* Forel 1913:307 ♀ ♂ n. syn.  
 = *cylindrica* Forel 1922:88 ♀ n. syn.  
 = *lata* Santschi 1930:53 ♀ n. syn.  
 = *recta* Santschi 1937:72 ♀ n. syn.  
 (T) *sechellensis* Forel = *parallela*  
 (T) *septentrionalis* Clark = *turneri*  
 (T) *sinuata* Roger 1860:297 ♀ ♂ Panama to N Argentina E of Andes [17]  
 = *minerti* Forel 1905:156 ♀ n. syn.  
 = *boliciana* Santschi 1921:83 ♀ n. syn.  
 (T) *strenua* Wheeler & Mann 1914:6 ♀ Haiti [17]  
 (T) *subtilis* Emery = *parallela*  
 (T) *suturalis* Forel = *lamellosa*  
 (T) *tasmaniensis* (Forel) \* = *turneri*  
 (T) *tenuis* Emery 1899:467 ♀ ♀ W Africa [1]  
 (T) *thwaitesi* Donisthorpe = *elyptata*  
 (T) *tricuspidata* Emery 1901:665 ♀ Sumatra; Malaya [11]  
 = *penangensis* Wheeler 1929:29 ♀ n. syn.  
 (T) *tritschleri* Forel = *parallela*  
 (T) *turneri* Forel 1895:420 ♀ N. Queensland to Tasmania; SW Australia [16]  
 = *tasmaniensis* (Forel) \* 1913b:176 ♀ n. syn.  
 = *bicolor* (Clark) \* 1930:11 ♀ n. syn.  
 = *reticulata* (Clark) \* 1934:33 ♀ n. syn.  
 = *septentrionalis* (Clark) \* 1934:34 ♀ n. syn.  
 (T) *victoriae* Forel = *parallela*  
 (P) *viehmeyeri* Santschi 1913:429 ♀ E Africa [8]  
 (T) *wroughtonii* Forel = *parallela*  
 (T) *zodion* Brown n. sp. ♀ Ecuador [18]

## Key to Species of African *Platythreya* (Workers)

- Opening of propodeal spiracle round or oval ..... 2  
Opening of propodeal spiracle elongate, slit shaped (fig. 29) ..... 8
- Size large, trunk length (WL)<sub>1</sub> > 3.8 mm (E. Africa) ..... *cribrinodis*  
Size smaller, WL < 3.8 mm ..... 3
- Posterior margin of petiolar node completely unarmed; mandibles with masticatory borders toothless, cultrate; head width (eyes omitted) < 0.9 mm (Natal) ..... *cooperi*  
Posterior margin of petiolar node armed with 2 or 3 blunt teeth or angles; mandibles finely but distinctly toothed or crenulate; head width (eyes omitted) usually 0.9 mm or more ..... 4
- Head width (eyes omitted) < 1.0 mm; in full-face view, scapes fail to reach posterior margin of head (W Africa) ..... *tenuis* [1]  
Head width (eyes omitted) > 1.0 mm; in full-face view, scapes overreach posterior margin of head at least slightly when held straight back from insertions ..... 5
- Second segment of antennal funiculus about twice as long as third, and much longer than eye (W & C Africa) ..... *occidentalis* [6]  
Second segment of antennal funiculus about the same length as third, and much shorter than eye ..... 6
- Posterodorsal extremity of petiolar node between lateral teeth rounding downward into posterior face, or at least without a sharp projecting margin (figs. 18, 19); mandible near base with a strong dorsolateral groove ..... 7  
Posterodorsal extremity of petiolar node with a sharply projecting margin that includes the 2 lateral teeth or angles and a low median tooth or lobe that overhangs the concave posterior face (figs. 21, 22); mandible without dorsolateral groove (W, E, & C Africa) ..... *modesta* [2]
- Sculpture opaque, with many conspicuous large punctures on petiole and other dorsal surfaces (E, C, & S Africa) ..... *schultzei* [5]  
Sculpture of dorsal surfaces fine and in part feebly shining; coarser punctures small and shallow, inconspicuous on petiole and other dorsal surfaces (W Africa) ..... *frontalis* [4]
- Eyes small, their maximum diameter ≤ greatest width of antennal scape in front view; petiolar node with sharp, strongly projecting posterodorsal margin (figs. 29, 30; C Africa) ..... *gracillima* [13]  
Eyes much longer than greatest scape width; posterodorsal border of petiolar node not or only weakly projecting caudad ..... 9
- Posterior face of petiolar node concave, sharply distinct from dorsal surface, and slightly overhung by the weakly projecting posterodorsal border; mesonotum not at all impressed (C & E Africa to Rhodesia) ..... *arnoldi* [8]  
Posterior face of petiolar node convex or flat, continuing the rounded dorsal face; mesonotum often impressed, at least weakly and in part ..... 10
- Petiole long and narrow, width/length index < 64; mesonotum distinctly impressed over its whole length (S into C Africa; nests in ground) ..... *lamellosa* [8]

- Petiole not so long and narrow, width/length index > 64; mesonotum at most feebly impressed in posterior part, where it joins metanotum ..... 11
11. Size large, trunk length (WL) > 3.8 mm (W & C Africa; nests in hollows in trees) ..... *conradii* [7]  
Size smaller, WL < 3.8 mm (Angola; nest habitat unrecorded) ..... *crucheti* [7]

## Key to the *Platythyrea* of Madagascar (Workers)

Posterior margin of petiolar node –

- Forming 2 large, blunt teeth, excised between ..... *bicuspis* [15]  
Forming 3 strong, triangular teeth ..... *moqueyssi* [3]  
Forming a rim without conspicuous toothlike processes ..... *arthuri*

## Key to Indo-Australian *Platythyrea* Species (Workers and Queens)

1. Petiolar node seen from directly above longer than broad, or rarely about as broad as, or even slightly broader than, long, but always much narrower than pronotum; maxillary palpi short, not extending much beyond buccal cavity ..... 2  
Petiolar node seen from above much broader than long (W at least 1.25×L), nearly, or quite, as broad as pronotum; maxillary palpi very long, extending almost to foramen magnum (figs. 31, 33; Australia) ..... 8
2. Posterodorsal border of petiolar node strongly projecting caudad; as seen from above, emarginate or excised in the middle so as to form 2 teeth or lobes (figs. 24–26) ..... 3  
Posterodorsal border of petiolar node bearing 3 strong, acute teeth (fig. 16; Malaya; Sumatra; Borneo) ..... *tricuspidata* [11]  
Posterodorsal border of petiolar node unarmored (figs. 1, 17) or obtusely tridentate to merely sinuate (figs. 14, 27) ..... 6
3. Propodeum armed with a pair of short teeth or tubercles (fig. 20) ..... 4  
Propodeum unarmed; dorsum curving evenly into declivity in side-view outline (figs. 23, 28) ..... 5
4. Length of basal segment of funiculus > maximum diameter of eye > length of second funicular segment; eye large in worker, greatest diameter > 0.30 mm; head broad, CI > 91 (India) ..... *sagei* [14]  
Length of funicular segment II > maximum diameter of eye, which is subequal to length of basal funicular segment; greatest diameter of eye < 0.30 mm; head narrower, CI < 91 (New Guinea; Borneo; Malaya) ..... *quadridentata* [14]
5. Posterodorsal border of petiole with a broad, deep excision separating 2 distinct though blunt teeth (figs. 26, 28; Philippines) ..... *bidentata* n. sp. [13]  
Posterodorsal border of petiole rounded, interrupted only by a small, shallow median emargination (figs. 23, 24; SE Asia, Ceylon) ..... *clipeata* [13]
6. Petiolar node (above spiracle) slightly higher than long, and as

wide as, or slightly wider than, long; posterodorsal border narrowly rounded into, and slightly overlapping, posterior face, but immarginate and unarmed (fig. 17; Philippines) ..... *inermis* [12]

Petiolar node (above spiracle) longer than high and longer than wide, its posterodorsal border marginate and bearing low vestiges of 3 teeth, or at least sinuate as seen from above (figs. 14, 27) ..... 7

7. Head elongate, wide behind and narrowed anteriorly (CI < 77), with deeply excavated posterior margin and strongly advanced, oval, free clypeal margin (fig. 37; Nicobar Is.) ..... *nicobarensis* [10]  
Head not markedly elongate (CI > 77) and with only shallowly concave posterior margin; free clypeal margin broadly and gently convex (Seychelles Is. and India to Philippines; Polynesia; E Australia) ..... *parallela* [9]

8. Petiolar node brownish red, contrasting with dark brown of head and gaster (E, S, and SW Australia); see discussion ..... *turneri* [16]  
Head and body unicolorous brown or ferruginous; see discussion [16] ..... 9

9. Color dark brown; most standing hairs of dorsal body surfaces < 0.08 mm long; posterodorsal margin of petiolar node unarmed in the middle (SW Australia) ..... *micans*  
Color yellowish ferruginous; most standing hairs of dorsal body surfaces > 0.10 mm long; posterodorsal margin of petiolar node with a sharp, upturned median tooth (SW Australia) ..... *dentodinis*  
Color ferruginous, appendages and legs brown; posterodorsal margin of petiolar node with a weakly indicated median tooth (S Australia; Reevesby I.) ..... *brunneipes*

## Key to New World *Platythyrea* Species (Workers)

1. Larger species; head width across and including eyes > 0.90 mm ..... 2  
Smaller species; head width across and including eyes < 0.90 mm ..... 6
2. Base of mandible with a distinct curved sulcus that originates at the insertion on the dorsal side and soon runs obliquely forward to the lateral margin (fig. 43) ..... 3  
Base of mandible without such a sulcus, or the sulcus indistinct and obscured by pubescence or limited to a short section close to the insertion (fig. 42) ..... 5
3. Larger species; petiolar node > 0.85 mm long ..... 4  
Smaller species; petiolar node < 0.85 mm long (Mexico; C. America; W. Indies; S Florida) ..... *punctata*
4. Head > 1.4 mm wide, including eyes; petiolar node only slightly longer than broad (Haiti) ..... *strenea*  
Head < 1.4 mm wide, including eyes; petiolar node much longer than broad (fig. 41; Panama to Bolivia E of Andes) ..... *sinuata*
5. Femora of prothoracic legs very strongly swollen, greatest width > 38% of length (figs. 39, 45; Trinidad; Guianas; Orinoco–Amazon Basins) ..... *angusta*  
Femora of prothoracic legs only about 1/4 as wide as long (WL < 38%) (figs. 38, 44; tropical S America; rare or absent in much of the range of *P. sinuata*) ..... *pilosula*



6. Head long and relatively narrow (eyes excluded and clypeus included),  $CI < 80$ ; clypeus swollen and convex in middle; posterior margin of petiolar node as seen from above with lateral corners produced caudad as short, blunt teeth or angles (N Mato Grosso) ..... *exigua*  
 Head short and broad,  $CI > 80$ ; clypeus nearly flat, free margin feebly emarginate in the middle (fig. 36); posterior margin of petiolar node with broadly rounded, unarmed lateral corners (figs. 34, 35) ..... *zodion* [18]  
 Occasional samples from South America in couplets 2-5 do not key out well and are possibly hybrids or intergrades. See discussion [17].

## Probolomyrmex

- > *Probolomyrmex* Mayr, 1901:2-3, ♀. Type: *Probolomyrmex filiformis* Mayr, 1901, monobasic. Taylor, 1963:345-365, revision.  
 > *Escherichia* Forel, 1910:245, ♀. Type: *Escherichia brevispinis* Forel, 1910, monobasic. Syn. Taylor, 1965:346.

This genus was well and comprehensively revised by Taylor in 1965, and I find no reason to cover the same ground. Since his revision, however, 2 new species, *P. bidens* and *P. proce* [19, 20], have come to light, and the status of some old ones [21] require discussion, so that a revised species list and a few comments and records are offered here.

In his generic diagnosis, Taylor characterizes the worker-sting as "well developed," which scarcely does justice to the powerful structure as seen fully or nearly fully extruded in the syntype of *P. dammermani* (MCZ) reviewed by him. In this specimen, the extruded sting shaft is 0.52 mm long, with a thick base, as compared to a total gastric length of only 1.13 mm. A worker specimen of *P. dammermani* was dissected, and proved to be without the stridulatory file on the pretergite of gastric segment II, a condition I believe holds throughout the genus because of the "tight" fit of the second segment into the first gastric segment of all 9 species I examined externally for this character. The modal constriction between the first and second segments is seen clearly in side view, but is not usually apparent in dorsal view. The second gastric segment is not "fused" into a tube, as Taylor indicates; instead, the tergum and sternum separated easily and cleanly along lateral sutures, with only slight tension in a *P. dammermani* worker treated with KOH.

The characters distinguishing *Probolomyrmex* from *Platythyrea* are cited in comparative form on p. 7.

## PROBOLOMYRMEX species

- (T) *angusticeps* M. R. Smith = *boliviensis*  
 (T) *bidens* Brown n. sp. S India [19]  
 (T) *boliviensis* Mann 1923:16 ♀ Bolivia; Panama [21]  
 = *angusticeps* M. R. Smith 1949:39 ♀ n. syn.  
 (T) *brevispinis* (Forel) 1910:246 ♀ E Africa [21]  
 = *parvus* Weber 1949:3 ♀ n. syn.  
 (T) *dammermani* Wheeler 1928:7 ♀ Java; Philippines  
 (T) *filiformis* Mayr 1901:3 ♀ S Africa  
 (T) *gracilis* Taylor 1965:358 ♀ & ♂ E Australia  
 (P) *guineensis* Taylor 1965:353 ♀ W Africa [22]

- (T) *palauensis* (M. R. Smith) 1953:127 ♂ to *Leptanilla* (Taylor 1965)  
 (T) *parvus* Weber = *brevispinis*  
 (T) *petiolatus* Weber 1940:76 ♀ Panama; Colombia [21]  
 (T) *proce* Brown n. sp. S India [20]  
 (T) *salomonis* Taylor 1965:358 ♀ Solomon Is.

## THE CERAPACHYINAE OR PRODORYLINAE

Over the last half century the Cerapachyinae, first raised by W. M. Wheeler (1902, 1920) to subfamily rank, have gradually come to be accepted as a taxon at that level. Wheeler (1922) removed the tribe Cylindromyrmecini (*Cylindromyrmex* and *Simopone*) to subfamily Ponerinae, but Brown (1954) later returned these genera to Cerapachyinae. At this stage, the Cerapachyinae were back to equivalence with Emery's "Sectio Prodorylinae" of the Genera Insectorum (1911).

In this fundamental work, Emery divided the Ponerinae into 3 sections, with these characterizations:

- Prodorylinae: Larva uniformly hairy, without piligerous tubercles. Male: mandibles well developed, genitalia completely retractile, subgenital plate deeply forked, cerci lacking.  
 Proponerinae: Larva uniformly hairy, without piligerous tubercles. Male: mandibles well developed, genitalia usually nonretractile, subgenital plate entire, cerci developed. (*Parapone* with a furcate subgenital plate of special form; *Myrmium* without cerci.)  
 Euponerinae: Larva with piligerous tubercles. Male: mandibles more or less reduced, genitalia not retractile, subgenital plate entire, cerci developed.

When Emery wrote this, of course, the larvae and males of only a few ponerine species had been studied, so it is not unexpected that some exceptions to these characterizations have been found as our knowledge has grown. In spite of this, the classification has proved useful right up to the present time. In fact, the characters Emery gave for Euponerinae are in general those of the tribe Ponerini, in which I include Leptogenyini, Odontomachini, and perhaps Thaumatomyrmecini (Brown 1963 and in preparation).

Note that Emery's separation of Prodorylinae from Proponerinae depends wholly upon characters of the male terminalia. To this set may be added a worker-female character, the denticulate margination of the pygidium (figs. 2, 5, 52, 104; Brown 1954), found in all of the prodoryline genera. A first impression that the Cerapachyinae (= Prodorylinae) form a compact monophyletic group is further strengthened by the habitus of the workers, especially as seen in life. All are elongate, parallel-sided, heavily sclerotized forms, with exceptionally short, thick antennae inserted close together at the front of the head. The antennae are actively vibrated ahead in a wasplike way as the living ant moves along. Add to this our knowledge that species in different genera are raiders of ant or termite colonies, and we have an apparently complete picture of taxonomic solidarity and distinctness.

Another aspect of cerapachyine taxonomy is the old theory, neatly expressed in Emery's name "Prodorylinae,"

that these genera form an evolutionary bridge connecting the Ponerinae to the Dorylinae. Probably the widespread acceptance of this theory led to subfamily rank for the intermediate taxon. Now, however, the conviction grows that the Dorylinae or true army ants are a diphyletic, and possibly even a triphyletic, group. If such an interpretation prevails, then to which, if any, of the dorylines were the cerapachyines ancestral? This is a problem currently under investigation, depending on deeper study of both dorylines and cerapachyines than has heretofore been possible.

Unavoidably, then, the problem of doryline ancestry falls also upon the cerapachyines, and for much the same reasons, raising the same question: Have specialized lifeways led to convergently similar life-forms? Once this question is asked, the mind turns immediately to some apparent faults in the classification of the tribes and genera within the Cerapachyinae.

Leaving aside for the moment the extensive synonymy called for among the genera close to *Cerapachys*, the most glaring anomaly in cerapachyine taxonomy is the inclusion of *Simopone* with *Cylindromyrmex* in a separate tribe *Cylindromyrmecini*. *Simopone*, despite superficial resemblances of some of its species to some *Cylindromyrmex* in structure of the head and in general body shape, clearly belongs with the *Cerapachys* group of genera. In fact, as we shall see, the very separation of *Cerapachys* and *Simopone* as genera comes into question. *Simopone* possesses, and *Cylindromyrmex* lacks, the angular carinae on the cheeks that characterize the *Cerapachys* group, and the posteroventral head region in *Simopone* is more like that of *Cerapachys* than *Cylindromyrmex* (figs. 93, 94).

Once *Simopone* is removed from its traditional position with *Cylindromyrmex*, the latter genus is seen in a new light. In fact, one can begin to understand why W. M. Wheeler removed *Cylindromyrmecini* to the Ponerinae, considering that he had by that time probably never seen a specimen referable to *Simopone*. With *Simopone* transferred to Cerapachyini, we find a very interesting biological situation.

The food of the reinforced tribe Cerapachyini, so far as known, is ants; *Cylindromyrmecini* (*Cylindromyrmex*) and *Acanthostichini* (*Acanthostichus*) are termite predators. Cerapachyini are well represented in the Old World, but meagerly in the New; *Cylindromyrmex* and *Acanthostichus* are endemic to the New World. *Cylindromyrmex* is primarily a dweller in hollow twigs and other plant cavities; *Acanthostichus* is terrestrial, even hypogaean; these two genera share some basic resemblances in the worker-queen castes, but one doubts if they are really closely related to each other. Thus we arrive by steps at the concept of 3 separate tribes in Emery's section *Prodorylinae* of subfamily Ponerinae:

- (1) Cerapachyini (Old World and New World, raid nests of other ants).
- (2) *Cylindromyrmecini* (New World, feed on termites).
- (3) *Acanthostichini* (New World, raid nests of termites).

What about the phylogenetic positions of these 3 tribes? At the present stage of our knowledge, this is mostly guesswork. The idea that the Cerapachyini are related to Ectatommini is old, and still carries weight, but the derivation of the former from any living or known fossil genus of the latter is rendered unlikely by the maximum number of palpal segments (6 maxillary, 4 labial) in a cerapachyine being greater than in any ectatommine genus except *Acanthoponera*, which is an unlikely direct ancestor on other grounds. If Cerapachyini and Ectatommini are cognate tribes, we can conceive of an early split at which the worker-queen ectatommines kept many generalized characters and developed a morphological tendency towards a downwardly arched gaster, while the cerapachyines embarked on an evolutionary course as raiders of other ant species, a lifeway that may have dictated a straighter body axis allowing the rapid transport of prey and brood.

As for their evolutionary issue, Emery's notion that the Cerapachyini gave rise to the Dorylinae may have something to it still, even though the old conception of the army ants as a monophyletic taxon is fast fading. It is possible that *Eciton* and relatives in the New World and/or *Aenictus* in the Old World arose separately from cerapachyine ancestors. At the moment, we don't know enough to make more than wild guesses about these possibilities.

The *Cylindromyrmecini* may have been a direct offshoot of the Ectatommini. I have already pointed out the resemblance between *Gnamptogenys alfaroi* and some *Cylindromyrmex* species (Brown, 1958:301-302). We need to know more about males and larvae of *G. alfaroi* and of *Cylindromyrmex* before we can say more about this possible relationship, which may after all be only another example of convergence, based on this case on termiterous lifeways.

The place of *Acanthostichini* in the ponerine phylogeny remains obscure. I have considered *Amblyoponini*, *Ectatommini*, and *Typhlomyrmecini* in turn as possible acanthostichine ancestors, but the evidence for each of these origins is as yet insufficient to be convincing. *Acanthostichini* and *Cylindromyrmecini* may after all be fairly close together, and both need much more study.

Kusnezov (1959) believed that the Old World myrmicine genus *Metapone* is related to *Acanthostichus*, but it seems much more likely that such similarities as exist between these genera are due mainly to convergence based on their termite-hunting proclivities. Taylor (*in litt.*) has suggested that *Metapone* is a specialized stock related to *Vollenhovia*, and this is a good possibility.

There is at least one alternative to the 3-tribe arrangement of the prodorylines that is worth some thought. This alternative would consider all 3 of the stocks to belong to one phyletic lineage corresponding to Emery's *Prodorylinae* (plus the later-discovered *Leptanilloides*). This lineage could be considered as a tribe or as a subfamily (to be called Cerapachyini or Cerapachyinae), but probably a designation as a tribe within subfamily Ponerinae would better suit these specialized predators.

However that may be, the Cerapachyini as known at present have a rather distinctive larval mandible, in which the apical portion is acute and bordered on the masticatory margin by a series of minute teeth or denticles in place of the 2 large subapical teeth of more primitive ponerines. The larval mandible of *Acanthostichus* as figured by Emery (see below) appears to fit the cerapachyine pattern, though the figures available are not exactly comparable in orientation.

Although we need to know better the details of mandibular shape for a wider variety of species and genera, the information we now have indicates that the larval mandible of "Prodorylinae" and army ants are similar in a general way, though it is not known how this *Bauplan* is adaptive for either prodoryline or doryline lifeways.

Of the 3 tribes, the larvae of only the Cerapachyini have been subjected to modern comparative study. Two species of *Acanthostichus* were briefly described and sketchily figured by Emery (1899a:4; see also G. C. Wheeler 1950: 109-110) and Bruch (1925), but the larva of *Cylindromyrmex*, despite strenuous efforts to obtain materials, remains undescribed except for very brief remarks by W. M. Wheeler (1924a).

To deal with the situation for now, I have recognized Cerapachyini, Cylindromyrmecini, and Acanthostichini as separate tribes within Ponerinae, mainly because this course tends to leave the question of their phyletic interrelationships open. The alternative treatment, placing them all in a single tribe (or subfamily) apart from the other tribes of Ponerinae, implies either a confidence in the hypothesis that all of these lineages sprang from a single "prodoryline" stock, or else the acceptance of a possibly polyphyletic taxon. In the present instance, I am forced to be skeptical of the monophyletic hypothesis, and I think a polyphyletic taxon would only aggravate confusion and misunderstanding.

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## TRIBE CERAPACHYINI

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**Worker:** Essentially monomorphic, though often with a considerable range of sizes in a single species and even in a single nest series. Smaller workers tend to have allometrically narrower heads and usually lack ocelli; larger workers apparently grade into ergatoid queens in many species and have 1 or all 3 ocelli; in some species, all workers have 3 ocelli.

Integument hard and thick, smooth, or variously sculptured, in most species at least partly punctate. Color of full adults ranging from yellow through red or brown to black, dark species sometimes with a blue opalescent overlay. Pilosity of simple, fine, tapered hairs, sparse and short to fairly abundant and long; sometimes specialized into a shorter pubescence that may be dense on limited parts of the body.

Head unremarkable in form, usually slightly to considerably longer than broad, with subparallel, moderately convex sides and transverse posterior border; cervical border concave. Undersides of posterior corners of head on each side with a carina that extends forward for a greater or lesser distance in most species (fig. 93). Frontal lobes sometimes lying horizontal or only obliquely raised, and separated, but more commonly sharply raised or vertical and contiguous, with the frontal carinae fused behind.

Compound eyes varying from very large (and placed in anterior, middle, or posterior position on sides of head) to small or even absent.

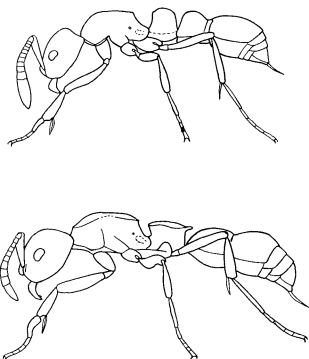
Antennae thick, with short clavate scapes and clavate funiculi, 9-12 segments total, inserted near front of head. Apical segment largest. From each antennal insertion a more or less flat or concave area extends laterad and is bounded near the side of the head by a curved or angled carina that runs forward across the cheek and ends at the lateral wing of the clypeus (figs. 46, 67). Clypeus narrow, crowded by the anteriorly displaced frontal lobes and antennal insertions, and extending back between these lobes only when they are separated, a condition found in a minority of species; free margin of clypeus depressed, usually with a small, rounded median lobe (often translucent). The flat area around the antennal insertion sometimes extends forward as a flat angulate or rounded process from the anterior clypeal margin on each side of the middle.

Mandibles short, thick, downcurved, subtriangular, with convex outer borders, distinct basal and masticatory borders meeting at an angle; masticatory border edentate, crenulate, or obscurely dentate; when closed, held close to clypeus.

Under mouthparts (see Gotwald, 1969:43-48, plates 29, 30, 32) compact; stipites heavily sclerotized, each with a transverse groove; labrum broader than long, bilobed, with an anteromedian notch.

Palpi ranging from maxillary 6- to 2-merous (1-merous in *Leptanilloides*) and labial 4- to 2-merous; it is possible that some of the many subterranean species not yet dissected have fewer segments in one or both pairs of palpi. The most common formulae seem to be maxillary 2 or 3, labial 2 segments.

Trunk rigid and box-like, the dorsal sutures obsolete or nearly so, except in the 2 fossil species and very rarely in extant species, which have a deeply cut and possibly flexible promesonotal suture. Dorsal surface convex to nearly flat, in some groups of *Cerapachys* marginate dorsolaterally and constricted in the middle as seen from above; propodeum with a distinct dorsum and declivity, the latter often marginate, but unarmed. Propodeal spiracle usually round or elliptical, rarely a slit, placed low, near or below level of trunk axis. Bulla of metapleural gland distinct. Posterior coxa often with genual plates well developed, and sometimes with the mesal plate extended as a prominent, rounded, translucent dorsal lobe (fig. 3).



Figures 3 and 4. *Cerapachys* workers in side view to show habitus of different species groups. 3: *C. opacus*, *dohertyi* group. 4: *C. cohici*, *turneri* group (formerly *Phyracaeae*) (after E. O. Wilson).

Posterior tibiae each with a single pectinate apical spur; middle tibiae with or without a smaller apical spur, usually pectinate when present. A second, smaller tibial spur is present in *Cerapachys crawleyi* on both middle and hind legs. Tarsal claws in most species slender and simple, but in a minority of species, the claws each have a submedian tooth, or may even be subpectinate, that is, with a basal lobe or tooth in addition to the submedian tooth.

Petiolar node sessile, various in shape with the species, with or without anterodorsal and dorsolateral margins. Postpetiole a clearly defined segment separated front and rear by constrictions from the adjacent segments, and varying in relative bulk by comparison with these segments so as to appear either as a virtual part of the gaster (*Sphinctomyrmex*) or as a second node in the waist (*Cerapachys typhlus* group), as in Myrmicinae or some army ants (e.g. *Eciton*, *Neivamyrmex*, *Aenictus*). All intermediate conditions exist in various cerapachyine species, so that the tribe as a whole forms a morphocline from the 1- to the 2-segmented waist often used to distinguish subfamilies among the Formicidae. (See figs. 91, 95, 99, 100). The postpetiole usually, however, has a well-developed, convex sternum.

More or less correlated with the variation in postpetiolar size and proportions is the wide variation in form of the gaster among cerapachyine genera and species; this also forms a rough morphocline. In most *Sphinctomyrmex*, the first 3 gastric segments after the postpetiole are similar in size and distinctly set off by intersegmental constrictions.

In *Cerapachys*, the first gastric segment (true abdominal segment IV) dominates the succeeding segments, and this tendency is carried to an extreme in the *C. typhlus* group in such species as *biroi* (fig. 95) and *edentata*, where the first segment covers nearly the whole of the gaster, and the succeeding segments are reduced and crowded into an apical position, as in most Myrmicinae.

Pygidium usually impressed discoid, the laterapical borders with raised edges furnished with a row or a field of minute acute denticles; these may be reduced to only 4 or 6 denticles in some presumably arboreal (*Simopone*) species, but they are usually more numerous. In *Leptanilloides*, in which the pygidium is reduced and shifted to a ventral position, the denticles are absent. Sting present and functional, usually well-developed, but no sign of an exerted sting in the 3 *Leptanilloides* specimens available.

**Queen:** Normal (i.e., winged when virgin, with large eyes, ocelli, and developed pterothorax), or ergatoid to various degrees in different species, or even in a single colony. The boundary between worker and queen is especially vague and problematical in this tribe. In *Sphinctomyrmex*, ergatoidy in some species has begun to converge toward the dichthadiiform condition of army ant queens, which are characteristically without eyes and ocelli, have broadened head and petiole, reduced wingless trunk, and relatively large gaster. Often more than one ergatoid is found in a colony, but it is not known whether these are all functional reproductives. In most species, queens resemble large workers in size, sculpture, and color, as well as in details of the mouthparts, etc.

Wings, when present, basically of the ponerine pattern, but with thick, broad, heavily pigmented pterostigma, and often with veins weak or shortened in the apical half. Reduction of venation is notable in some smaller species.

**Male:** (Unknown for *Leptanilloides*.) Similar to the conspecific queen in size and robustness, or a little smaller; head shorter, more nearly globular, with very large, semiglobose eyes. Frontal carinae a reduced copy of those of conspecific workers, usually forming half-rings around inner front sides of antennal sockets; clypeus broad and usually with translucent, rounded median apron on the free margin. Mandibles well developed, triangular, fig. 96; (falcate in some *Sphinctomyrmex*, figs. 97-98), edentate, meeting or crossing when closed. Antennae geniculate, 13-merous, occasionally 12-merous, with scape short, not reaching beyond ocellar triangle, but still decidedly longer than funicular segments I, II, and III, and usually longer even than apical segment; the last sometimes slightly incrassate, but in general the antenna is slender and without the strong club of the worker and queen; pedicel very short, much shorter than succeeding funicular segment (II). The strong curved or angulate cheek carinae of the workers are not developed in the males. Palpi in the few species examined like those of worker.

Trunk moderately developed; notauli present in some species of *Sphinctomyrmex* (e.g., *asper*), but weakly developed

or absent in most other known species. Wings with rather weak venation, ranging from complete ponerine pattern to lacking most distal elements back to midlength (fig. 92); pterostigma usually large, heavily sclerotized and dark in color; hind wing without anal lobe. Legs robust; mid-tibiae with 2, 1, or 0 apical spurs, and hind tibiae with 1, rarely 2, pectinate spurs. Tarsal claws with submedian tooth in some species, rarely (some *Simopone*) with a second lobe or tooth, but usually the claws are simple.

Petiole usually simple, with a subcuboidal, dome-shaped or elongate-rectangular node. Postpetiole simple, a little smaller than following (first gastric) segment, and separated from it by a weak to strong constriction; gaster usually more or less cylindrical, slightly downcurved, with or without constrictions between segments (*Sphinctomyrmex*), or narrowed segmental bases amounting to constrictions (e.g., in *Cerapachys augustae*). Subgenital plate very diverse in different species-groups, but usually with bilateral points or spines, often forming a "fork" (figs. 114–116, 118, 120–122). In some Australian species of the "*Phyracces* groups," the bidentate condition is lost or nearly lost (fig. 116). Genital capsule with all main parts (parameres, volsellae, aedeagus) present, but very diverse in form with genus and species (figs. 123–129). The sample available is still too small and unrepresentative to allow the analysis of phylogenetic trends and group characters, and it sometimes seems that intrageneric variation is more extreme than it is among genera. The figures at least serve to show the variety of forms among the genitalia; further analysis will, of course, require mesial views of the separated parts. Note that even within single genera, parameres may be separated into basal and distal pieces (gonocoxites and gonostyli?), as in figs. 123 and 127; or not, as seen in figs. 124 and 129. In a few species (*Sphinctomyrmex*) the pygidium is margined and truncate; in some others, denticulate margins occur.

Sculpture and pilosity varies with the species, but most have some smooth and coarsely punctate areas, with unremarkable, fine pilosity. Color variable, often black or brown, but sometimes bicolorous.

**Larvae:** G. C. Wheeler (1950) and G. C. and J. Wheeler (1964, 1973, 1974) have published descriptions, mostly with figures, of 11 species of Cerapachyini (4 *Cerapachys*, 4 "*Phyracces*", 1 "*Lioponera*", 1 "*Eusphinctus*", and 1 *Simopone*). Their key to genera in the 1964 paper (p. 67) is based entirely on hair form. Clark (1923) gives data and figures on larval hairs for 2 species of "*Eusphinctus*." These hairs are bifid, trifid, or 6-branched, but very young larvae may have simple hairs. In the same paper, Clark gives hair shape for 2 species of "*Phyracces*" as bifurcate, with head hairs simple in at least one species.

The 1964 and 1973 papers by the Wheelers show that *Cerapachys edentata* (= *australis*) has both bifid and simple hairs on both head and body; body hairs may show secondary branching. Nearly the full range of Cerapachyini hair types (including hairs absent) is shown by the genus

*Cerapachys* in the old sense (i.e., excluding *Phyracces* and *Lioponera*), and it is evident that even though only a small, poorly representative fraction (at most 10% of the species) of cerapachyine larvae has been looked at, this sample fails to show a convincing division into generic lines on larval characters, at least on the characters that have thus far been emphasized. Even the few long, hooked hairs ringing each somite of the *Lioponera luzuriagae* larvae look like only a species or species-group character, adaptive in twig-inhabiting forms, and even some of these larvae had bifurcate body hairs in some samples examined (G. C. Wheeler 1950), though they were thought to be dried-out specimens.

**Pupae:** So far as known, normally enclosed in cocoons.

#### BIONOMICS OF CERAPACHYINI

Two of the 4 genera of Cerapachyini (*Cerapachys*, *Sphinctomyrmex*) include a number of species that have been observed raiding the nests of other ants (see especially Wheeler 1918; Clark 1923, 1924, 1941; Wilson, 1958). I can add observations on *Cerapachys mayri* and *C. lividus* in the rain forest of Madagascar, and on *C. indicus* in the Western Ghats of southern India. All 3 *Cerapachys* species were found attacking, or returning from attacks on, nests of *Pheidole* species, and the booty being transported consisted of larvae, pupae, pharate adults, and even in some cases dead but fully pigmented *Pheidole* soldiers and workers. These raids were all observed in progress near midday in shaded situations, and the raiding workers returned one by one over logs and roots along an obvious odor trail with their prey.

In Australia, a raid of *C. clarki* was observed in 1951 in open eucalypt woodland at Berrimah, near Darwin, Northern Territory, over bare soil against a nest of a small *Iridomyrmex* in bright morning sunlight. This raid was very loose and involved only 3 or 4 *Cerapachys* workers while I watched it, so it may have been the final stages of an action begun much earlier.

A raid of *Sphinctomyrmex steinheili* observed by me in Victoria, Australia (Wilson, 1958:136) was waged against a small *Stigmatoceros* (Formicidae) species during the afternoon; the *Sphinctomyrmex* ran over bare soil, but took advantage of cracks in the earth where they could. The *Stigmatoceros* workers were seen scattering and hiding on pieces of eucalypt bark and dead leaves lying on the ground, often carrying their own larvae. Their behavior recalled that of *Formica fusca*- or *pallidifusca* group species raided by *F. sanguinea*-group slavemakers in the Northern Hemisphere, and may imply the use of "propaganda" allomones such as those sprayed by the slavemakers to spread panic in the slave *Formica* colonies they are attacking (Wilson and Regnier, 1971). The behavior of army ant prey ant species is also often of the "panic flight" kind, so army ants should also be investigated for propaganda allomones. It seems that actual combat has rarely or never been observed in

raids of *Cerapachys* on prey ants in nature, but the damaged and blackened antennae and legs of *Sphinctomyrmex imbecilis* series taken by Clark in southwestern Australia [71] testifies to possible struggles between the raiders and potential prey.

An *S. caledonicus* colony fragment observed over several weeks in an artificial (plaster-bottomed) nest was placed in contact with a colony fragment of *Acanthomyops claviger*, a North American formicine that *Sphinctomyrmex* would of course never normally meet in nature. (The *Acanthomyops* defends itself with formic acid spray and terpenoids such as citrinellal.) The *Sphinctomyrmex* raided the adjacent *Acanthomyops* colony, were duly sprayed and smeared with the noxious allomones, but nevertheless returned to their chambers with *Acanthomyops* adults and brood as prey. The *Sphinctomyrmex* workers spent an inordinate amount of time grooming themselves and their nestmates, especially just after raids—evidently a behavior pattern aimed at removing the toxic substances they receive from prey species.

The *Sphinctomyrmex* workers and ergatoids also spend a great deal of time in the nest with their long, flexible bodies wrapped around their own brood, thus forming round, dense clusters that may fill large chambers.

The prey of several species of *Cerapachys* living in forested areas of the Old World is usually recorded as small or medium-sized species of *Pheidole*, but Wilson has also recorded *Strumigenys* and *Lordomyrma* (Myrmicinae) species serving as prey in Melanesian forests, while species of *Iridomyrmex* (Dolichoderinae) and *Melophorus* (Formicinae) are raided in more arid, open parts of Australia.

Species of the *longitarsus* group (= *Lioponera*) tend to nest in hollow twigs, beetle burrows, or other channels in wood, branches, or bark, and it is possible that they are all arboreal or subarboreal. *C. singaporensis* was taken originally nesting in a hollow mango twig. *C. foreli* has been taken by Raigier and van Boven in hollow twigs in Zaïre (personal communication), and I have found this species climbing a tree trunk in sparse single file in a copse in the Dabou Savanna, Ivory Coast.

*Simopone* species also appear to be dwellers in hollow twigs. Raigier and van Boven wrote me that they found *S. schoutedeni* and *S. conciliatrix* in such microhabitats in Zaïre; Bolton took *S. conciliatrix* in hollow cacao twigs in Ghana [77], and Arnold (1915) reported *S. marleyi* from hollow stalks of castor bean plant in Natal, South Africa. Bequaert (label data) took an *S. grandis* [76] from a palm trunk in a central African swamp forest. No one has reported the food habits of *Simopone*, but this genus is so closely related to *Cerapachys* that it too may be ant predatory.

Most species of *Cerapachys* and *Sphinctomyrmex* appear to nest in the ground or in rotten wood. Nests I have seen in moist forested areas usually have one or a few relatively capacious chambers connected to the surface by a short passage, but in arid areas, there may be several chambers

10–50 cm or more deep in the soil, with longer tunnels. Sometimes the nest is under a rock. The entrance is usually an inconspicuous hole without a crater, but in a few cases, a small crater or turret occurs at the surface.

Nest populations can contain as few as 20 adult workers to more than a thousand; the higher counts hold for some species of *Sphinctomyrmex* and the *Cerapachys typhlus* and *antennatus* groups, but most *Cerapachys* nests probably contain less than 200 workers. Pupae are normally enclosed in cocoons. The winged males are very active when mature and may attempt to take flight when the nest is opened.

The means of nest-founding of cerapachyines is unknown. In southwestern Australia, Clark (1923, 1924) found solitary individuals of *C. angustatus* and *C. constrictus* under a stone and a log respectively, and thought that the latter, at least, was founding a nest. However, it is not even certain that these specimens were reproductives, let alone founding queens, since no brood was found with either one, and both are “ergatoid” (i.e., possibly worker) in form.

The more advanced and probably more army-ant-like species of *Sphinctomyrmex* (*imbecilis*, *froggatti*, *perstictus*, *trux*, *mjobergi*, etc.) apparently have a single, more or less dichthidiform queen, although the picture is confused by the appearance in some of these species of additional “ergatoid” forms that could just possibly have some reproductive function. It is such species that probably have the males with falcate mandibles (see p.31).

In other species with dealate or less completely modified reproductives (e.g., *steinheili*, *duchaussoyi*, *asper*, *occidentalis*) each nest may contain several, up to 20 or more, of these ergatoid queens. Of course, we do not know how many such individuals in a given nest may function as true reproductives, or to what extent, if they do so function.

Whether cerapachyines are nomadic is an open question. To me, the nests I have seen look impermanent, and the broods show a strong tendency to be synchronized, like those of army ants and nomadic Ponerinae (*Onychomyrmex*, *Simopelta*). Nomadism in an ant-preying ant could well be adaptive, to avoid depleting the food supply in a given neighborhood, just as it is in the army ants. In the cerapachyines we probably see the early stages of developing army ant lifeways, and it is probably no accident that cerapachyines are relatively so abundant in Australia, where army ants are rare and local, and apparently are late arrivals on the continent (2 species of *Aenictus*).

The feeding habits of genus *Leptanilloides* are unknown. This genus is known from a single collection made by Mann at Tumupasa in northern Bolivia, “from beneath a deeply embedded stone near a stream.” The collection consisted of “a small series of workers, taken with callows, but without sexual or immature phases”—a circumstance that could apply to a raiding column.

**DISTRIBUTION:** The Cerapachyini are primarily Old World inhabitants and are widespread there in tropical

and warm-temperate areas, in Africa, Madagascar, and the Oriental and Australian areas (including Melanesia as far as Fiji). The tribe is unknown in Europe and the U.S.S.R., but it would not be surprising to find that hypogaic species exist in some of the warmer parts of central Asia. Two or more species reach central China and Japan in eastern Asia.

In the New World, cerapachyines are nowhere very common, but a few species are known from the warm deserts of southwestern United States and northern Mexico, from forest country in Mexico, and very sporadically in South America south to Bolivia and southeastern Brazil. The details of distribution are cited under each genus below.

## GENERA OF CERAPACHYINI

As here conceived, the Cerapachyini form a compact and distinctive, albeit extensively radiated, tribe of 4 genera. The synonymy is extensive at the generic-subgeneric level, and most of it has been proposed during the last few years in various places by different authors, mainly on the basis of my investigations, which were proceeding piecemeal over the years. As a result, the synonymies got published in faunal and other nonrevisionary studies, and usually without proper justification and discussion. Evidence for the synonymies is given under each senior synonym, but a few important matters are discussed immediately following the synoptic summary:

### 1. *Cerapachys*

- = *C. subgenus Syscia*
- = *C. subgenus Oceraea*
- = *C. subgenus Cysias*
- = *C. subgenus Parasyssia*
- = *Lisoponera*
- = *Procerapachys*
- = *Phyracaces*
- = *Chrysapace*
- = *Neophyracaces*

### 2. *Simopone*

### 3. *Sphinctomyrmex*

- = *Eusphinctus s. str.*
- = *Eusphinctus subgenus Nothosphinctus*
- = *Eusphinctus subgenus Zasphectus*
- = *Atthiophone*

### 4. *Leptanilloides* (transferred from Ecitoninae)

The relationships of *Simopone* and *Sphinctomyrmex* to *Cerapachys* are very close, and for the first genus, the situation is discussed under genus *Cerapachys*, below. *Sphinctomyrmex* is separated from *Cerapachys* by only one formal character: the constriction between the main segments of the relatively elongate gaster. One might add that these principal gastric segments are subequal in length in "typical" *Sphinctomyrmex* (figs. 99, 104, 113). But this generic character is partly compromised by the India-Burma species *S. furcatus* (and the closely related *S. taylora*, which may be only a nanitic variant of *furcatus*), which has somewhat less pronounced constrictions between gastric segments than do other *Sphinctomyrmex* species, in addition to which the first gastric (fourth true abdominal) segment is

clearly larger than the next 2 segments (compare figs. 99 and 100). *S. furcatus* thus makes transition between *Sphinctomyrmex* and *Cerapachys*. The putative male of *S. furcatus* is intergradient in the same character, but is distinct in having only 12 antennal segments, vs. 13 for the other known males of *Cerapachyini*.

I have pondered this dilemma long and hard, and have decided to give *Sphinctomyrmex* the benefit of the doubt. The long, jointed gaster of *Sphinctomyrmex* appears to be adaptive, inasmuch as it is used to wrap around and help protect the brood. It is possible, though, that *Sphinctomyrmex* will later split into 2 or 3 genera on the basis of male and queen characters, as discussed under the genus below. Division now would be entirely premature.

*Leptanilloides* appears to be an isolated neotropical derivative from a *Sphinctomyrmex* stock.

## Key to Genera of Cerapachyini (Workers)

1. Principal segments of gaster (true abdominal segments IV, V, VI) separated by marked constrictions and subequal in size (except in 2 India-Burma species in which IV is distinctly larger) (figs. 99, 100, 102, 108, 113) ..... 2  
Gastric segments not separated by marked constrictions after the one behind the postpetiole (abdominal segment III); first gastric segment (abdominal IV) much larger than those following (figs. 5, 47, 49, 51, 59, 75, 83, 91, 95, 103) ..... 3
2. Pygidium (tergum of last externally visible gastric segment = true abdominal segment VII) exposed dorsally; pointed, rounded, or excavated, and armed with numerous minute spinules (figs. 2, 99-102; *S. Brasil*; Old World tropics to temperate Australia) ..... *Sphinctomyrmex*  
Pygidium displaced to a ventral position, unarmed (extremely small and slender workers, *Leptanilloides*-like in appearance, known only from a single collection in Amazonian Bolivia) ..... *Leptanilloides*
3. Tibiae of middle pair of legs with apical spurs (world tropics and warm-temperate areas) ..... *Cerapachys*  
Tibiae of middle pair of legs without apical spurs (Old World tropics) ..... *Simopone*

## *Cerapachys*

- > *Cerapachys* F. Smith, 1857:74, ♀. Type: *Cerapachys antennatus*, monobasic.
- > *Cerapachys*: Emery, 1902:24, subgeneric classification and relationships, new spp. described.—1911:8, diagnosis and subdivision into subgenera, species list.
- > *Cerapachys*: Arnold, 1915:11-17, *S. African* spp., key and diagnoses.
- > *Cerapachys*: Mann, 1921:408, key to workers of Fijian spp.
- > *Cerapachys*: Borgmeier, 1957:107, discussion of subgenera, with doubts expressed about their validity; New World spp. listed; *Cerapachys* neuter in gender after Follett, 1955:10.
- > *Cerapachys*: Wilson, 1959:39-57, discussion, description, list of spp. and key to spp., Melanesia.
- > *Cerapachys*: Kempf, 1972:76, list of neotropical species; *Syscia* and *Parasyssia* synonymized on p. 7.
- > *Cerapachys* Schultz, 1906, *Spolia Hymenopt.*, p. 155, invalid emendation of *Cerapachys*.
- > *Syscia* Roger, 1861:19. Type: *Syscia typha*, monobasic. Synonymized

- with *Cerapachys*, Kempf, 1972:7.
- > *Cerapachys* subgenus *Syscia*: Wilson, 1959:39, 44-45, 51-52, 54-55, Melanesian species, with keys.
  - > *Syscia*: Wilson and Taylor, 1967:33, Polynesian sp., species synonymy.
  - > *Ooceraea* Roger, 1862:248. Type: *Ooceraea fragosa*, monobasic. Synonym of *Cerapachys*, teste Brown, 1973:183.
  - > *Cerapachys* subgenus *Ooceraea*: Emery, 1902:24. —1911:10, ♀, diagnosis, species list.
  - > *Lioponera* Mayr, 1878:666. Type: *Lioponera longitarsus*, monobasic. Synonym of *Cerapachys*, teste Brown, 1973:181.
  - > *Lioponera*: Emery, 1911:11-12, ♀ & ♂.
  - > *Lioponera*: Donisthorpe, 1939:252-257, review and species list.
  - > *Parasyria* Emery, 1882:235. Type: *Parasyria biochardi*, monobasic. Synonymized with *Cerapachys* in Kempf, 1972:7.
  - > *Cerapachys* subgenus *Parasyria*: Forel, 1892:343.
  - > *Cerapachys* subgenus *Parasyria*: Emery, 1902:22-24. —1911:9, ♀ & ♂, diagnosis, species list.
  - > *Phyracchys* Emery, 1902:23. Type: *Cerapachys mayri*, by original designation. —1911:10-11, pl. 1, fig. 3, ♀ & ♂, diagnosis, species list. Synonym of *Lioponera*, teste Brown and Taylor, 1970:957-958; synonym of *Cerapachys*, teste Brown, 1973:181.
  - > *Phyracchys*: Arnold, 1915:17-19, 3. African species.
  - > *Phyracchys*: Wheeler, 1918:215-216, discussion of affinities, etc.; 220-223, generic characters, distribution, etymology; 239-263, figs. 7-17, descriptions, review and key to species of Australia. —1922:22.
  - > *Phyracchys*: Clark, 1923:73, 78-89, normal and ergatoid queens, larvae, pupae; 7 spp. described from SW Australia. —1924:75-89, pl. 6-7, ♀ & ♂ biology, 8 Australian species described. —1930:3-6, 3 Australian spp. described. —1934:22-27, 6 Australian spp. described. —1941:71, 74-76, 2 Australian spp. described.
  - > *Phyracchys*: Wilson, 1959:55-56, keys and lists, New Guinea and New Caledonia spp.
  - > *Cerapachys* subgenus *Phyracchys*: Forel, 1902:405, 407. —1915:18-21, 3 Australian spp. described.
  - > *Cerapachys* subgenus *Cysias* Emery, 1902:24. Type: *Ooceraea papuana*, by original designation. Synonymized with *Cerapachys* subgenus *Syscia* by Emery, 1911:10.
  - > *Procerapachys* Wheeler, 1914:27-28. Type: *Procerapachys annuus*, by original designation. (Fossil in Baltic Amber.) New synonym.
  - > *Chrysapachys* Crawley, 1924:380-383, "apterous female," "recte ♀ or ergatoid ♀." Type: *Chrysapachys jacobsoni*, by original description, monobasic. Synonym of *Cerapachys*, teste Brown, 1973:179.
  - > *Cerapachys* subgenus *Chrysapachys*: Wheeler, 1924:225.
  - > *Neophyracchys* Clark, 1941:71, 76. Type: *Phyracchys clausi*, by original designation. Synonym of *Cerapachys*, teste Brown, 1973:183.

There has been a good deal of confusion about the gender of the name *Cerapachys*. Actually, words in Greek for "horn" containing the stem equivalent of *ker-* occur in all 3 genders, masculine, feminine and neuter. *Keras* is the neuter form, and *kerus* is the masculine form. When Smith named the genus, he seems to have been a bit careless in using an "a" instead of an "o" for the fourth letter, but his original employment of the name as masculine is clear from the masculine ending given to the name of the type species (*antennatus*) in adjectival form. Thus, there seems to be little room for argument, other theories (Borgmeier 1957) notwithstanding, and we should regard *Cerapachys* as masculine.

**Worker:** With characters of tribe. Postpetiolar segment (true abdominal segment III) strongly constricted from body of gaster and varying greatly from species to species in size relative to petiole and to true abdominal segment

IV, which always is the largest gastric segment. In the more extreme forms of the *fragosus* and *edentatus* groups, the petiole and postpetiole form 2 nodes that are small in comparison to segment IV, which covers and forms most of the gaster as in most Myrmicinae. (Compare figs. 91 and 95). No strong constriction between principal gastric segments.

Antennae 9-12 segmented, often with a swollen apical segment. Palpi segmented 4,3 to 2,2. Compound eyes varying from large and multifaceted to completely absent. Ocelli present in workers in a minority of species.

Tibial spurs on middle legs; tarsal claws simple or with a submedian tooth.

**Queen:** Usually winged, but sometimes wingless and ergatoid, always with compound eyes present so far as known, though they may be very small. Characters otherwise as in the worker of the same species, but body usually a little broader, segment for segment.

Wings, when present, like those of male.

**Male:** See characterization under tribe Cerapachyini (p. 15). So far as known, the male of *Cerapachys* always has 13-merous antennae and apical spurs on the mid-tibiae, and the mandibles are triangular, though often with acute apex and concave masticatory border. A sampling of genital capsules is shown in figs. 123-126, and subgenital plates in figs. 115, 116, 118, and 122.

In the discussion that follows, I shall show that the synonymy of *Cerapachys* extends very widely — much more widely, in fact, than I would have believed before I began this study. Nevertheless, all but one of the generic or subgeneric names here listed as synonyms of *Cerapachys* were based on species originally included in *Cerapachys*, or early assigned to *Cerapachys s. lat.* by Emery or Forel. Thus in a sense we are returning to an earlier generic concept.

The 4 subgenera of *Cerapachys* were based primarily on the number of antennal segments, thus: *Cerapachys s. str.*, 12 segments; *Parasyria*, 11; *Ooceraea*, 10; and *Syscia*, 9. The subgenus *Cysias* had already been synonymized under *Syscia* by Emery (1911:10).

The series *Cerapachys s. str.* — *Syscia* formed a rough morphocline, not only in the decline of antennal segment number from 12 to 9, but also in the loss of eyes in the worker, and in the reduction of the postpetiolar segment and relative increase in dominance of the succeeding (first gastric) segment. The most extreme result of these trends is seen in such *Syscia* species as *edentatus* and *biroi*, in which the petiole and postpetiole are similar in size, and the succeeding segment, true abdominal tergum IV, is enlarged to cover most of the gastric dorsum (fig. 95). This arrangement is formally like that of the subfamily Myrmicinae, and clearly represents a convergence to the myrmecine condition. It also renders very difficult the use of "waist" characters for the separation of formicid subfamilies in classifications and keys, especially when one has to distinguish certain army ants with 2-segmented waists from cerapachyines and myrmecines.



While the general morphocline in species-groups of *Cerapachys* involves reductions in both eye size (ommatidial count) and antennomere number, the reductions do not occur with complete concordance. Undescribed species with 12 antennomeres and dot-like eyes in the worker have been found in Africa and Asia, and in these same two continents we have large-eyed species (e.g., *nitidulus*) with 11 antennomeres. *C. kodecorum* new species from southeastern Kalimantan (Borneo) usually has 11 segments in the worker, but one worker from the same series has 7 or even only 6 abnormally thick segments in the funiculus. Who is to say really what is normal and abnormal in antennal segmentation in this genus?

In some 11-segmented species, the basalmost ring segments are often exceedingly short and indistinct, especially the first segment after the pedicel. This segment may even be largely hidden inside the pedicel, and may be partly fused with the succeeding segment (funiculus III). I believe that subgenus *Ooceraea*, based on 2 supposedly decamerous species, is actually cryptically 11-merous. At least, the type and other specimens of *O. fragosus* [65] seem to me to be obscurely 11-merous, but when the ambiguities of counting and of determining which segments are fused or partly fused become this great, antennal segment number has weakened taxonomic value. Borgmeier (1957:107), and after him Kempf (1972:7), apparently hold the same opinion. *C. fragosus* and relatives from Asia, described and undescribed, are so much like the 9-segmented *C. typhlus* group ("subgenus *Syscia*") in body form, sculpture, and postpetiolar-gastric proportions that it seems absurd to recognize *Syscia* merely on the flimsy antennal segment character.

The main characters supposed to separate *Phyracces* and *Lioponera* from *Cerapachys* are the proportions of the segments near the end of the antenna, and the shape of the petiolar node. In *Cerapachys*, the apical antennomere is usually very long and thick, even egg-shaped, and can be said to form a club of a single segment. While there can be no denying that many species fit the *Cerapachys* antennal pattern, others do so less well. The *antennatus* group (including *antennatus*, type species of *Cerapachys*), for example, shows wide variation in this character, tending to bridge the gap between the *Cerapachys* condition, with a very thick apical segment, and the *Phyracces* condition, in which the apical segment is little or not at all thicker than the penultimate segment.

The 5-merous club cited as a character of *Lioponera* seems to me completely ambiguous, as already discussed above. We also have such "bridging" species as *C. crawleyi* [24] and *C. lividus* [36]. Figures 87-90 illustrate the *Cerapachys*-*Lioponera*-*Phyracces* morphocline for antennal clubbing.

The character involving the petiolar node really boils down to whether the node is margined on the sides above. *Phyracces* species usually have strong dorsolateral margins on petiole and trunk, and the margination often extends to

the postpetiole and even, in a few Australian species, to the head behind the eyes. Thus one finds a morphocline for strength and extent of margination along the body axis within *Phyracces*, and this morphocline stretches of course into *Lioponera* (*C. longitarsus* group), which has only the petiolar node laterally marginate. Here again the *antennatus* complex of forms provides a bridge between *Cerapachys* and *Phyracces*, because in this complex, the petiole can be more or less *Phyracces*-like or *Cerapachys*-like in different-sized individuals of the same nest series. I have pointed out in the discussion of this group [25] that one species was originally described as "*Phyracces vandermeermohri*," which illustrates the ambiguity of the generic lines here. In addition to the *antennatus* group, we have the annectant forms *crawleyi* [24], *pruinosis* [60], and *lividus* [36]. Had the last-named species been earlier described from Australia instead of Madagascar, I believe it would have been put into *Phyracces* rather than *Cerapachys*.

The ambiguity of the margination as a generic character is also demonstrated in the descriptions of such species as *Phyracces pygmaeus* and *P. aberrans* [33, 47] (Clark, 1934: 25-27) and *P. braytoni* (Weber, 1949:3). I have examined the type of *P. braytoni* [34], and find it to be a member of the same species-group as *Lioponera longitarsus*, type species of that genus, and *P. pygmaeus* is actually a synonym of *longitarsus*. R. W. Taylor recognized independently (personal communication) that *Lioponera* was nothing more than an indistinct species-group within *Phyracces*, and we accordingly tacitly synonymized the latter in our contribution to "The Insects of Australia" (Brown and Taylor, 1970). The name *Lioponera*, being older, or course then took priority over *Phyracces*. The members of the *longitarsus* group are, so far as we know, arboreal or subarboreal dwellers in hollow twigs and perhaps other tubular cavities in wood or bark, a microhabitat in consonance with the workers' slender, cylindrical body build and large compound eyes. I assume that they prey on ants of other species occupying similar habitats, but there is no real information available on their feeding habits. Both *Lioponera* and *Phyracces* are treated as synonyms of *Cerapachys* in Brown (1973:181).

Clark (1941) raised a genus *Neophyracces* for a group of Australian species in which the workers normally possess ocelli. Most of these species are relatively large in size and prevalently bright orange or reddish ferruginous in color, and they seem especially well adapted to xeric conditions. Otherwise, they conform to the "typical" *Phyracces* pattern, with strongly developed margination of the trunk, petiole, and even the postpetiole. A number of *Phyracces* species in Australia are like them, except that the workers lack ocelli. Elsewhere in the collective genus *Cerapachys*—as in the complexes of *C. antennatus* [25] and *C. fragosus* [65]—the appearance of ocelli is an allometric character within as well as between colony series. Some of the large, ocellate individuals may in fact be functional reproductives (ergatoids), even in species known to possess dealate queens, but

at present we have no direct information on this matter. In view of our scanty and largely ambiguous knowledge of ocellar occurrence and function in *Cerapachys s. lat.*, it does not seem to me that Clark's *Neophracacae* is worthy of recognition as more than a species-group within *Cerapachys*. It would be interesting to know whether and to what extent the ocellate workers of this group also function as reproductives.

*C. crawleyi* illustrates one method of dealing with annectant species: make it the type of a new genus. This species was originally described by Crawley as *Chrysaspis jacobsoni* (*Chrysaspis*, like *Phyracacae*, is an anagram of *Cerapachys*). While the species [24] is aberrant in its own right, it fits fairly comfortably in either *Cerapachys* or *Phyracacae* as they have been constituted in recent years, and Wheeler (1924) doubted that it was outside of *Cerapachys*. However, *C. crawleyi* has one very primitive character in addition to its striking sculpture: the middle and hind tibiae each have a large and a small apical spur. The evidently related species *C. sauteri* has not been examined for the spur character, but if the tibiae in this poorly known Taiwanese species also have 2 spurs each, it may be necessary to resurrect *Chrysaspis* as a genus.

We still have to account for the genus *Simopone*. Although described by Forel in 1891 as a genus, *Simopone* was placed as a subgenus of *Cerapachys* by its author in the following year, but Emery's 1911 treatment of it as a genus set apart in a special tribe with *Cylindromyrmex* tended to obscure the early relationship. Most of the species subsequently described in *Simopone* tended to strengthen the concept of a separate genus; the 11-merous antennae, large, flat eyes, presence of ocelli, and above all, the separated frontal carinae, often framing demisclerites for the antennae, tended to mark off a presumably arboreal group of species with its own distinctive habitus. However, the central African species *grandis* [76] is not so typical, and the fact that it combines traits of *Cerapachys* and *Phyracacae* with those of more characteristic *Simopone* species was obscured by a mediocre original description and by the paucity and isolation of material available for study in collections. The discovery and analysis of another specimen of *grandis* [76] permits us now to say that it is such a strong link between *Simopone* and *Cerapachys s. lat.* that the generic distinction comes into doubt.

Further trouble for this distinction comes in the form of a new species, *Simopone conciliatrix* [77], *Simopone*-like in habitus, but with 12 antennomeres and other details that put it in the category of annectants between *Simopone* and *Cerapachys*. Of course, there exist species of *Cerapachys* with 11 antennomeres (subgenus *Parasyscia*), but, as already discussed, they mostly have the eyes reduced or absent, rather than enlarged as in *Simopone*. Thus the 11-merous condition in *Simopone* and *Parasyscia* has apparently been considered (by anyone who may have thought about it at all) as convergent. The new 12-merous species now ties

*Simopone* back to the more primitive line of *Cerapachys*, which (according to Williston's Rule) must have had 12 antennal segments. Williston's Rule may also be invoked in the matter of the maxillary and labial palpi, which in *C. grandis* have 6 and 4 segments respectively, but in *C. conciliatrix* only 3 and 2. We see here the expression of an interesting tendency in ants as a family to maintain high palpal counts among some epigaeic, and especially arboreal, foragers. In these same lines, however, antennal segments may either be reduced in number, or stay at the primitive number 12.

In the circumstances, my instincts have been to place *Simopone* in the synonymy of *Cerapachys* as a primitive arboreal group of the latter genus, and this is the way the situation may well be viewed by future revisers. There does, however, remain one character by which the two groups can still be unequivocally separated in at least the worker-queen castes, and that is the tibial spur of the middle leg — present in all *Cerapachys* I have examined, and absent in *Simopone*. Since the middle-leg spur character is concordant in a rough way with the traditional characters of *Simopone*, it seems best to continue to recognize the generic separation, a course that also avoids some awkward species-level homonymy that would result if the *Simopone* species were thrown into *Cerapachys*.

**BIONOMICS:** Discussed previously under the tribe.

**DISTRIBUTION:** *Cerapachys* as here constituted is by far the largest genus in the tribe, and its geographical range is virtually coterminous with that of tribe Cerapachyini. The genus is much better represented in the Old World than the New, and the majority of species, both described and undescribed, are in the Indo-Australian region. Forms with laterally margined petiole (formerly *Phyracacae*, *Neophracacae*, and *Lioponera*) are restricted to the Old World, and have radiated especially extensively in Australia, where they occur in semidesert as well as wet and dry forest habitats. The 9-segmented group (*Syscia*) is widespread in northern and eastern Australia as one or two species [63], and also has endemic species in New Guinea, the Solomons and Fiji; *S. birovi* of this group has become established in Hawaii and even in the West Indies, following probable overseas transport by human commerce. The 9-segmented species are good colonizers.

It is interesting to note that the "more typical" *Cerapachys* — the species with rounded petiole and 12 or 11 antennal segments related to *C. dohertyi* and *C. cribrinodis* — have not penetrated continental Australia, though they have spread through Melanesia as far eastward as Fiji. This absence may be related to the extraordinary radiation in Australia of *Sphinctomyrmex* in the adaptive zones that elsewhere are mainly occupied by *Cerapachys*.

In the New World, where *Sphinctomyrmex* is known only from a single rare, localized species, *Cerapachys* is represented sparsely by a few 11-segmented species ranging from Sonoran North America southward to Panama; one 11-

segmented species apparently isolated in southeastern Brazil; and one 12-segmented, minute-eyed species from Trinidad that possibly could be a historic immigrant like *C. biro*, known from the same island. The 11-merous species from North and Central America appear to be endemic, and number perhaps as many as 5 or 6, counting undescribed samples; these form a tightly knit group of blind or minute-eyed forms related to *C. augustae*. It seems likely that *Cerapachys* is limited in the New World by competition with myrmecotherous ecitonines such as *Neiomyrmex*.

In Africa, *Cerapachys* is widely and fairly well represented by a diversity of groups of species with 11 or 12 antennal segments (mainly 12) in habitats ranging from rain forest to arid karroo veld, montane grassland, and Saharan oases and wadis. Although at least one species (*C. piochardi*) occurs in the Middle East, no cerapachyine is known to reach Europe.

*Cerapachys* ranges to the southern shores of Australia and South Africa, and is well represented on Madagascar, but is still unknown from south of Brazil to South America. In Asia, the genus reaches north to the Himalayan wall, central China, and southern Japan.

# **CERAPACHYS species**

New combinations, formerly: \**Phyracces*, \*\**Neophyracces*,

†*Lisoponera*, †*Procerapachys*

- aberrans* (Clark)\* 1934a:25 ♀ N Queensland [47]
- (T) *adamus* Forel 1910a:18 ♀ N Queensland [46]
- aegyptius* Brown n.n. for *cooperi* (Donisthorpe) Egypt [33]
- = *cooperi* (Donisthorpe)† 1939:255 ♀ (preocc.)
- (T) *affer* Forel 1907a:9 ♀ E & S Africa [27, 30]
- = *cooperi* Arnold I 1915:14 ♀ n. syn.
- (T) *aikeni* Forel 1900b:332 ♀ India
- alfieri* (Donisthorpe)† 1939:256 ♀ Egypt [33]
- angustatus* (Clark)\* 1924:76 ♀ SW Australia
- annosus* (Wheeler)† 1914:28 ♀ fossil, Baltic Amber
- (T) *antennatus* F. Smith 1857:74 ♀ Sarawak [25]
- = *uhoeleri* Crawley 1926:389 ♀ n. syn.
- arnoldi* Forel 1914:211 ♀ S Africa [30]
- = *heavittii* Arnold 1926:192 ♀ n. syn.
- (T) *augustae* Wheeler 1902:182 ♀ Texas-Arizona [66]
- (T) *australis* (Forel)† 1895 = *longistarsus*
- (T) *australis* Forel 1900 = *edentata*
- bakeri* (Wheeler & Chapman)† 1925:55 ♀ Basile I. [60]
- (T) *beyrichi* Brown n. sp. ♀ S India [64]
- (T) *hicolor* (Clark)\* 1924:77 ♀ SW Australia
- (T) *hicolor* (Wheeler & Chapman)† 1925 = *longistarsus*
- (T) *binodis* Forel 1910a:20 ♀ N Queensland [48]
- (T) *biro* Forel 1907a:7 ♀ Nepal & C China to SE Asia; introd. to Polynesia & W Indies [63]
- = *silvestrii* Wheeler 1909:269 ♀ n. syn.
- = *sinensis* Wheeler 1928:3 ♀ n. syn.
- = *seini* Mann 1931:440 ♀ n. syn.
- = *terensis* Weber 1939:94 ♀ n. syn.
- (T) *brachynodus* Forel = *mayri*
- (T) *braunsi* (Emery)\* 1902:27 ♀ S Africa [29]
- (T) *braytoni* (Weber)\* 1949:3 ♀ C Africa [34]
- (T) *brevicollis* (Clark)\* 1923:78 ♀ SW Australia
- (T) *brevis* (Clark)\* 1924:78 ♀ W & C Australia [49]
- (T) *bryanti* Wheeler 1919:47 ♀ Sarawak [33]
- (T) *butteli* Forel = *sulcinodis*

- (T) *castaneus* (Clark)\* = *clarki*
- (T) *centurio* Brown n. sp. C Africa ♀ [30, 31]
- ceylanicus* Motschulsky 1863:22 to *Tetraponera* (Emery 1921:25)
- (P) *clarki* (Crawley)\* 1922:433 ♀ Australia, widespread [40, 44]
- = *castaneus* (Clark)\* 1924:79 ♀ ♀ n. syn.
- (T) *clans* Forel 1893 to *Sphinctomyrmex*
- (T) *clans* (Clark)\* = *princeps*
- (P) *coecus* (Mayr) 1897:420 ♀ Ceylon [63]
- cochii* (Wilson)\* 1957:1 ♀ New Caledonia
- (T) *congolensis* (Forel) = *nkomenis*
- (T) *conseratus* Viehmeyer 1913:142 ♀ Celebes (copal) [54]
- constrictus* (Clark)\* 1923:79 ergatoid? SW Australia
- (T) *cooperi* Arnold I = *affer*
- (T) *cooperi* (Arnold) II\* = *vespula*
- cooperi* (Donisthorpe)† = *aegyptius*
- (T) *coxalis* (Arnold)\* 1926:193 ♀ Rhodesia
- (?) *crassus* (Clark)\* 1941:74 ♀ Australia: NW Victoria
- (T) *crawleyi* Wheeler 1924b:225 ♀ Sumatra; Borneo; Philippines [24]
- = *jacobsoni* (Crawley) 1924:381, ♀ (recte ♀) n. syn.
- = *mirandus* Wheeler 1924b:224 ♀ n. syn.
- (T) *cribrinodis* Emery 1899b:463 ♀ W & C Africa [30]
- (T) *cryptus* Mann 1921:408 ♀ Fiji
- davisi* M. R. Smith 1942:64 ♀ SW U.S. [66]
- (T) *decarsei* (Santschi)† 1912:150 ♀ Chad [33]
- (T) *despoina* Wilson 1959:45 ♀ Papua
- dehertzi* Emery 1902:25 ♀ Borneo; Sumatra [53]
- = *parvulus* Emery 1902:25 ♀ n. syn. Wilson 1959:57
- (?) *dominus* Wilson 1959:46 ♀ New Guinea [52]
- (T) *dromas* (Clark)\* = *fervidus*
- dumbleni* (Wilson)\* 1957:5 ♀ New Caledonia [47]
- (T) *edentatus* (Forel) 1900a:69 ♀ E Australia [61]
- = *australis* (Forel) 1900a:68 ♀
- (T) *eidmanni* (Menozzi)\* = *nkomenis*
- elagens* (Wheeler)\* 1918:254 ♀ Australia: E New South Wales
- emeryi* Forel 1892 to *Simopone*
- emeryi* Forel 1893 to *Sphinctomyrmex* (preocc.)
- emeryi* (Viehmeyer)\* 1914:26 ♀ = ? (preocc.) S Australia [38]
- (?) *fausti* Arnold 1949:262 ♀ [30]
- favosus* (Wheeler)† 1914:31 ♀ fossil in Baltic Amber
- fermatidis* Motschulsky 1863:21 to *Tetraponera* (Emery 1921:25)
- (T) *fervidus* (Wheeler)\* 1918:245 ♀ Australia [42]
- = *leae* (Wheeler)\* 1918:243 ♀ n. syn.
- = *scrutator* (Wheeler)\* 1918:247 ♀ n. syn.
- = *neumani* (Clark)\* 1923:82 ♀ n. syn.
- = *fici* (Viehmeyer)\* 1924:222 ♀ ♀ n. syn.
- = *flavescens* (Clark)\* 1930:5 ♀ ♀ n. syn.
- = *dromas* (Clark)\* 1941:75 ♀ ♀ n. syn.
- (T) *fici* (Viehmeyer)\* = *fervidus*
- ficosus* (Wheeler)\* 1918:252 ♀ SE Australia [45]
- (?) *flammeus* (Clark)\* 1930:4 ♀ W Australia
- flavaeclavatus* Donisthorpe 1938:499 ♀ New Guinea [52]
- (T) *flavescens* (Clark)\* = *fervidus*
- (P) *foreli* (Santschi)\* 1914:309 ♀ W & C Africa [27]
- = *langi* (Wheeler)\* 1922a:54 ♀ n. syn.
- = *santschii* (Wheeler)\* 1922a:56 ♀ n. syn.
- = *occipitalis* (Bernard)\* 1952:216 ♀ n. syn.
- (T) *fossulatus* Forel 1895a:48 ♀ Ceylon [59]
- (T) *fragosus* (Roger) 1862:249 ♀ (recte ergatoid ?) Ceylon [65]
- (T) *fuscator* Mann 1921:410 ♀ Fiji Is., Taveuni (Wilson 1959:55)
- (T) *gilesi* (Clark)\* 1923:81 ♀ ♀ larva SW Australia
- grandis* (Clark)\* 1934a:22 ♀ S Australia
- gracilis* (Clark)\* 1934a:25 ♀ W Australia
- (?) *guyonethi* (Clark)\* 1941:77 ♀ Australia; NW Victoria
- (P) *hans* (Wheeler)\* 1918:240 ♀ Queensland
- (T) *heavittii* (Wheeler)\* 1919:48 ♀ ♀ Sarawak [51]

- (P) *hesitii* Arnold = *arnoldi*  
 (T) *hesitii* Donisthorpe = *cuscutatus*  
 (T) *hendurians* Mann 1922:1 ♀ ♀ Honduras; Belize [66]  
 (T) *terensis* Weber = *hiri*  
*imertensis* Forel 1891:138 ♀ Madagascar [37]  
 (T) *incomptus* Emery 1902:153 ♀ New Guinea [52]  
 (T) *incomptus* (Clark)\* = *incomptus*  
 (T) *incomptus* Brown n. n. for *incomptus* Clark SW Australia [43]  
 = *incomptus* (Clark)\* 1924:82 ♀ ♀ preocc.  
 (T) *indicus* Brown n. sp. ♀ S India [56]  
 (T) *jacobsoni* Forel 1912a:104 ♀ Java; Malaya; Sumatra; Borneo; Philippines [25]  
 = *sumatrensis* Crawley 1926:391 ♀ n. syn.  
 = *vanderseemohri* (Menozzi)\* 1932:2 ♀ n. syn.  
 (T) *jacobsoni* (Crawley) = *crawleyi*  
 (T) *jovis* Forel 1915:20 ♀ N Queensland [38]  
*kenyensis* Consani 1951:169 ♀ E Africa  
 (T) *kodecorum* Brown n. sp. ♀ SE Kalimantan [58]  
 (T) *kraepelini* Forel 1895b:246 ♀ Madagascar  
 (T) *kronbieni* (Donisthorpe)\* 1947:580 ♀ Papua  
 (T) *lamborni* Crawley 1923:29 ♀ C & E Africa [30]  
 = *pigra* Weber 1942:41 ♀ n. syn.  
 (T) *langi* (Wheeler)\* = *foreli*  
 (T) *larsatus* (Wheeler)\* 1918:257 ♀ SE Australia  
 (T) *latiuscula* Emery = *peringueyi*  
*latus* Brown n. n. for *reticulatus* Clark SW Australia  
 = *reticulatus* (Clark)\* 1926:45 ♀, preocc. Emery 1923  
*leae* (Wheeler)\* = *fervidus*  
 (T) *lindrothi* Wilson 1959:52 ♀ ♀ Fiji Is.:Viti Levu  
 (T) *lividus* Brown n. sp. ♀ Madagascar [36]  
*longicornis* Viehmeyer = *opacus*  
 (T) *longitarsus* (Mayr)† 1878:667 ♀ ♀ India to Philippines & N Australia [33]  
 = *australis* (Forel)† 1895c:422 ♀ n. syn.  
 = *parvus* (Forel)† 1900b:330 ♀ ♂ n. syn.  
 = *bicolor* (Wheeler & Chapman)† 1925:54 ♀ ♀ ♂ n. syn.  
 = *pygmaeus* (Clark)\* 1934a:26 ♀ n. syn.  
 (T) *luteovirgatus* Brown n. sp. ♀ ♀ Ceylon [57]  
 (T) *luzariagae* (Wheeler & Chapman)† 1925:53 ♀ ♀ Philippines  
 (T) *macrops* (Clark)\* 1941:79 ♀ Australia: N Victoria  
 (T) *majusculus* Mann 1921:408 ♀ ♀ Fiji Is.: Viti Levu  
 (T) *manni* Crawley 1926:390 ♀ Sumatra; Borneo [25]  
 (T) *marginatus* Emery 1897:594 ♀ New Guinea  
 (T) *mayri* Forel 1892a:244 ♀ Madagascar [37]  
 = *brachynodus* Forel 1892b:520 ♀ n. syn.  
 (T) *mirandus* Wheeler = *crawleyi*  
*mjobergi* Forel 1915:18 ♀ NW Australia  
 (T) *muiri* Wheeler & Chapman 1925:52 ♀ Philippines  
*multicavus* (Wheeler)\* 1918:251 ♂ W Australia [41]  
 (T) *natalensis* Forel 1901:335 ♀ S Africa:Natal [30]  
 (T) *negrosensis* Wheeler & Chapman = *rufigrator*  
*neotropicus* Weber 1939:93 ♀ Trinidad  
 (T) *neumani* (Clark)\* = *fervidus*  
 (T) *niger* (Santschi)† 1914:46 ♂ E Africa [33]  
 (T) *nigroventris* (Clark)\* 1924:84 ♀ ♀ SW Australia  
 (T) *nitens* Donisthorpe 1949:487 ♂ New Guinea  
 (T) *nitidulus* Brown n. n. for *nitidus* Weber C Africa  
 = *nitidus* Weber 1949:2 ♀ ♀ preocc.  
 (T) *nitidus* Wheeler & Chapman 1925 = *rufigrator*  
 (T) *nitidus* Weber = *nitidulus*  
 (T) *nkomoensis* (Forel)\* 1916:400 ♀ C Africa:Fernando Po I. [28]  
 = *congolensis* (Forel)\* 1916:401 ♀ n. syn.  
 = *eidmanni* (Menozzi)\* 1942:165 ♀ n. syn.  
 (T) *noctambulus* (Santschi)† 1910:70 ♂ Tunisia [33]  
 (T) *occipitalis* Bernard = *foreli*  
 (T) *oculatus* F. Smith 1857:74 ♂ to Myrmecinae [26]  
 (T) *opacus* Emery 1902:153 ♀ New Guinea  
 = *longicornis* Viehmeyer 1913:27 ♀ (syn. Wilson 1959:48)  
*papuanus* (Emery) 1897:594 ♀ New Guinea [62]  
 (T) *parvulus* Emery = *dohertyi*  
 (T) *parvus* (Forel)† = *longitarsus*  
*pavea* Mann 1919:277 ♀ Solomons [62]  
 (T) *peringueyi* Emery 1886:360 ♀ S Africa [30]  
 (T) = *latiuscula* Emery 1895:19 ♀ n. syn.  
 (T) *picipes* (Clark)\* 1924:86 ♀ SW Australia  
 (T) *pictus* (Clark)\* 1934a:23 ♀ Australia:W Victoria [38]  
 (T) *piger* Weber = *lamborni*  
 (T) *piliventris* (Clark)\* 1941:80 ♀ SE Queensland  
 (T) *piochardi* (Emery) 1882:235 ♀ Syria; Lebanon [35]  
 (T) *polynikes* Wilson 1959:50 ♀ New Guinea  
 (T) *potteri* (Clark)\* 1941:76 ♀ ♂ Australia:N Victoria  
 (T) *princeps* (Clark)\* 1934a:24 ♀ W & S Australia [39]  
 = *clarus* (Clark)\* 1930:3 ♀ ♀ n. syn. (preocc.)  
 (T) *pruinus* Brown, n. sp. ♀ Philippines:Negros I. [60]  
 (T) *pubescens* (Emery)\* 1902:26 ♀ Borneo; Sumatra [51]  
 (T) *punctatissimus* (Clark)\* 1923:84 ♀ ♀ SW Australia [44]  
*pusillus* (Emery) 1897:595 ♀ New Guinea [62]  
*pygmaeus* (Clark)\* = *longitarsus*  
*reticulatus* (Emery) 1923:60 ♀ Taiwan  
*reticulatus* (Clark)\* = *latus*  
*rhodesianus* Forel = *wroughtoni*  
 (T) *rizii* Forel = *julcinodis*  
 (T) *roberti* Forel = *wroughtoni*  
 (T) *rotula* (Forel)\* = *singularis*  
*rufigornis* (Clark)\* 1923:86 ♀ larva SE & SW Australia [46]  
 (T) *rufigrator* Wheeler & Chapman 1925:50 ♀ Philippines [55]  
 = *negrosensis* Wheeler & Chapman 1925:51 ♀ (syn. Brown 1955)  
 = *nitidus* Wheeler & Chapman 1925:52 ♀ (syn. Brown 1955)  
 (T) *rugulodis* (Wheeler)\* 1918:249 ♂ S Australia [40]  
 (T) *salmani* Karawajew 1925:72 ♀ Java  
 (T) *santschii* (Wheeler)\* = *foreli*  
*sauteri* Forel 1913c:187 ♀ Taiwan [24]  
 (T) *scutator* (Wheeler)\* = *fervidus*  
*sculpturatus* Mann 1921:407 ♀ Fiji Is.:Viti Levu  
 (T) *seini* Mann = *hiri*  
 (T) *senescens* (Wheeler)\* 1918:259 ♀ SE Australia  
 (T) *sibestrii* Wheeler = *hiri*  
 (T) *similis* (Santschi)† 1930:51 ♂ W Africa  
 (T) *simonsae* (Clark)\* 1923:87 ♀ ♀ larva SW Australia  
 (T) *sinensis* Wheeler = *hiri*  
 (T) *singaporensis* (Viehmeyer)\* 1916:110 ♀ gynandromorph, Singapore  
 (T) *singularis* Forel 1900a:69 ♀ SE Australia [38]  
 = *rotula* Forel 1910a:21 ♀ n. syn.  
 (T) *sjustedti* Forel 1915:18 ♀ NW Australia  
 (T) *splendens* Borgmeier 1957:107 ♀ SE Brasil  
 (T) *sudanensis* Weber 1942:42 ♀ S Sudan; Rhodesia [30]  
 = *variolus* Arnold 1949:261 ♀ n. syn.  
 (T) *sulcinodis* Emery 1899:493 ♀ S China; Himalayas; SE Asia to Philippines & Sumatra [25]  
 = *rizii* Forel 1892a:244 ♀ n. syn.  
 = *butteli* Forel 1913a:3 ♀ n. syn.  
 (T) *sumatrensis* Crawley = *jacobsoni* Forel  
 (T) *superatus* Wilson 1959:50 ♀ New Guinea  
 (T) *susculatus* (Viehmeyer)\* 1913:143 ♀ Malaya to Celebes & Philippines [50]  
 = *hesitii* (Donisthorpe)\* 1931:494 ♀ n. syn.  
 (T) *glycola* Arnold 1955:761 ♀ Rhodesia:Vumba Mts. [30]  
 (T) *terricola* Mann 1919:277 ♀ ♂ reinstated; Solomons [52]  
 = *talagi* Mann 1919:279 ♀ ♂ (syn. Wilson 1959:47)  
 (T) *tolteus* Forel 1909b:247 ♀ C America [66]  
 (T) *talagi* Mann = *terricola*  
 (T) *turneri* (Forel)\* 1902:405 ♀ C Queensland [46]

- (T) *typhlus* (Roger) 1861:20 ♂ Ceylon [65]  
*validus* Arnold 1960:79 ♀ Natal-Drakensberg Mts. [30]  
 (T) *vandermeermahri* (Menozi) \* = *jacobsoni* Forel  
*varians* (Clark) \* 1924:87 ♀ SW Australia  
 (T) *variolosus* Arnold = *sudanensis*  
 (?) *versicolor* (Donisthorpe)† 1948:589 ♂ New Guinea  
 (T) *vespula* (Weber) \* 1949:5 ♀ E & SE Africa [27]  
 = *cooperi* (Arnold) II \* 1915:18 ♀ n. syn.  
 (?) *villiersi* Bernard 1952:215 ♀ W Africa [30]  
 (T) *vitiensis* Mann 1921:406 ♀ Fiji Is.:Viti Levu  
*weeleri* Crawley = *antennatus*  
 (T) *wroughtoni* Forel 1910e:422 ♀ SE Africa [32]  
 = *rhodesiana* Forel 1913d:212 ♀ n. syn.  
 = *roberti* Forel 1914:212 ♀ n. syn.  
 (T) *zimmermani* Wilson 1959:54 ♀ Fiji Is.:Viti Levu

## Species groups of *Cerapachys*

The 137 unchallenged species of *Cerapachys* listed above may be placed in 18 informal groups. The groups are partly based on assumed phyletic relationships, and are drawn partly for convenience; they are all to some degree arbitrary, and do not all have equal phyletic rank. Accordingly, we may expect them to change as our knowledge grows.

We can arrange the groups into 2 main lineages, corresponding roughly to *Cerapachys* and to *Phyracces* (with *Lioponera* and *Neophyracces*) in the old classification.

### *Cerapachys* lineage

(sides of petiole immarginate)

#### *crawleyi* group [24]

*crawleyi*, *sauteri* (Oriental region)

#### *lividus* group [36]

*lividus* (Madagascar), intermediate between *Cerapachys* and *Phyracces* lineages

#### *antennatus* group [25]

*antennatus*, *jacobsoni*, *sulcinodis*, *manni* (Oriental region)

#### *annosus* group

*annosus*, *favosus* (fossil in Baltic Amber); large fossil species with large eyes and complete promesonotal suture

#### *wroughtoni* group [32]

*wroughtoni* (S Africa); small species, eyes minute or absent; promesonotal suture well developed

(The 5 groups above all have 12-merous antennae.)

#### *dohertyi-cribrinodis* group [30, 33]

The members of this group are dealt with in 2 series for convenience only; I see no way to split the group except along arbitrary geographical lines. African-Malagasy-Middle Eastern species ("cribrinodis group"): *ajfer*, *arnoldi*, *centurio*, *cribrinodis*, *faurei*, *imernensis* (11 antennal segments), *kenyensis*, *lambornii*, *natalensis*, *nitidulus* (11), *peringueyi*, *piochardi* (11), *sudanensis*, *sybicola*, *validus*, *villiersi*. Indo-Malanesian species ("dohertyi group"): *aikeni*, *bryanti*, *conservatus*, *desposyne*, *dohertyi*, *dominulus*, *flavaculatus*, *fossulatus* (11), *inconspicuus*, *indicus*, *kodecorum* (11), *lindrothi*, *luteoviger*, *majusculus*, *muri*, *opacus*, *polynikes*, *reticulatus*, *rufithorax*, *salimani*, *sculpturatus*, *superatus*, *terricola*, *vitiensis*, *zimmermani*. This is the dominant and most rapidly spreading and radiating group in

genus, except in Australia, and it seems to have given rise directly to the *fragosus* and *augustae* groups. All of the species listed above have 12-merous antennae, unless indicated specifically as 11-merous. In addition to the variation in antennal segment number, eye size varies greatly in this group; a number of species, both described and undescribed, have minute eyes.

#### *fragosus* group [65]

*besucheti*, *coecus*, *fragosus* (S Asia, particularly India and Ceylon); small species, eyes reduced or absent in workers; petiole and postpetiole small, first gastric segment very large; sculpture of small, crowded punctures; antennae 11-merous, sometimes appearing to be 10-merous; corresponds to old subgenus *Ooceraea*.

#### *typhlus* group [65]

*biroi*, *cryptus*, *edentatus*, *fuscior*, *papuanus*, *paua*, *pusillus*, *typhlus* (Indo-Malanesia, Australia; introduced elsewhere in tropics); with only 9 antennomeres; otherwise similar to *fragosus* group, from which it is probably directly descended. Corresponds to the old genus or subgenus *Syscia*.

#### *augustae* group [66]

*augustae*, *hondurians*, *tolteus* and some undescribed species (SW United States, south at least to Panama); workers with minute or no eyes, 11-merous antennae; males collected separately at light doubtless belong here also (*augustae*, *davisi*). Probably derived directly from *cribrinodis-dohertyi* group, and differentiated from it rather arbitrarily on geographical grounds.

miscellaneous neotropical species

*neotropicus* (Trinidad), *splendens* (SE Brasil); species with 12-merous antennae resembling members of *cribrinodis-dohertyi* group. It is possible that *neotropicus* is introduced from the Old World.

### *Phyracces* lineage

(sides of petiole marginate)

#### *fervidus* group [42]

*bicolor*, *brevis*, *elegans*, *fervidus*, *gilesi*, *incontentus*, *krombeini*, *latus*, *nigriuentris*, *picipes*, *simmonsae* (Australian, found mostly in open xeric or intermediate habitats; *krombeini* is from Port Moresby area of Papua-New Guinea). This is a heterogeneous group of red-and-black, yellow-and-brown, or plain reddish species, actually somewhat residual after other groups are excluded. Some of the species, such as *picipes*, are almost aberrant enough to be placed in groups of their own.

#### *turneri* group [46]

*adamus*, *binodis*, *cohici*, *ficosus*, *larvatus*, *marginatus*, *ruficornis*, *senescens*, *turneri* (mainly in forest areas of E and SW Australia, New Guinea, and New Caledonia); mostly small, predominantly black species, separated from the *fervidus* group mainly by color and modal habitat. Trunk margined along sides.

#### *aberrans* group [47]

*aberrans*, *dumbletoni* (Queensland, New Caledonia); black forest species lacking lateral margination on the trunk.

#### *singularis* group [38]

*brevicollis*, *crassus*, *flammeus*, *grandis*, *heros*, *jovis*, *mjobergi*, *pictus*, *singularis*, *varians* (Australia, mainly savanna, open woodland or desert areas); red or red-and-black species, often large in size, with the head marginate on the sides behind the eyes.

#### *clarki* group [40, 44]

*clarki*, *punctatissimus* (Australia); medium-sized, yellowish red species with punctate petiolar disc, found mainly in open woodland or arid scrub in W and N Australia.

#### *princeps* group [39]

*angustatus*, *constrictus*, *graevesi*, *gwynethae*, *macrops*, *piliventris*, *potteri*, *princeps*, *sjoestedti* (Australia, mainly in W and in arid inland parts of E and center; mainly reddish yellow species, often large in size; workers with 3 ocelli. Some species listed in this group may be based on ergatoid queens whose workers lack ocelli; if such forms exist, they rightly belong to the *fervidus* group. This group is the former genus *Neophracces*.

#### *mayri* group [27, 28, 29, 37, 50]

*braunsi*, *coxalis*, *foreli*, *kraepelini*, *mayri*, *nkomensis*, *suscitatus*, *vespula* (Africa and Madagascar; *suscitatus* is Oriental); mostly black or brown species, pubescence mostly undeveloped. This is a heterogeneous group separated from the Australian species mainly on geographical grounds.

#### *pubescens* group [51]

*hewitti*, *pubescens*, *singaporensis*, and some undescribed species (Oriental region); small, black or brown species with more or less abundant pubescence on the body — at least on postpetiole and gaster — in addition to the erect pilosity. This assemblage may make transition between the *mayri* and *longitarsus* groups.

#### *longitarsus* group [33, 34, 60]

*bakeri*, *braytoni*, *longitarsus*, *luzuriagae*, *pruinus* (Africa, Oriental Region to N Australia); the species roughly corresponding to the former genus *Lioponera*; small, slender, large-eyed, black, brown, or red-and-brown species with trunk immarginate on the sides. Probably all arboreal dwellers in hollow twigs, insect burrows in bark or wood, etc. Males assigned to *Lioponera* by Donisthorpe [33] may or may not belong here; see under "Lineage uncertain (males only)" below.

#### miscellaneous Australian males [40, 41]

*mullewamus*, *rugulinodis* (S and W Australia); these are yellowish males taken at light; they probably belong to *singularis*, *princeps*, *fervidus*, or *clarki* groups.

#### Lineage uncertain (males only)

##### miscellaneous (New Guinea)

*nitens*, *versicolor*: Since we cannot yet distinguish among males of most *Cerapachys* groups, it is impossible to assign these males taken away from worker or queen association.

##### miscellaneous (Africa) [33]

*aegypticus*, *alfierii*, *dorseti*, *niger*, *noctambulus*, *similis*: Probably these belong mainly to hypogaecic species of the *crinibodis* group or twig-inhabiting members of the *longitarsus* group.

Wilson (1959:40) recognized 5 species-groups of *Cerapachys* s. str. (i.e., with 12-segmented antennae) from the Indo-Australian region, but his groups are somewhat scrambled, partly due to misunderstandings about sculptural details gained from the literature. I think it is worthwhile to recognize only 3 groups for the same set of species: *antennatus* group, *dohertyi* group, and *crawleyi* group.

I have continued to recognize antennal segment number as one of the "diagnostic" group characters, but I am less and less impressed by it as used for this purpose, considering the probability that reduction has occurred more than once in the genus. *C. kodecorum* n. sp. [58], for example, seems to me more closely related on the basis of body form, sculpture, and pilosity to members of the *C. dohertyi* group — even to *C. dohertyi* itself — than it does to such other 11-segmented "*Parasyscia*" species as *C. piochardi*.

#### Phylogeny of *Cerapachys*

Although some likely phylogenetic relationships have been mentioned in the preceding group listings, the main lines of descent within the genus are unclear. We might expect the archetypal *Cerapachys* to have had a complete promesonotal suture, as in the Oligocene *annosus* and recent *C. urugthoni*; large compound eyes, as in *annosus* and many living species; 2 apical spurs on middle and hind tibiae, as in *C. crawleyi*, and a submedian tooth on each tarsal claw. We might also expect to have found 6,4 palpal segmentation, as in some *Simopone*. In fact, some of the larger extant *Simopone*, especially *S. grandis*, are near our idea of the *Cerapachys* archetype, but these particular species have only 11 segments in the antennae, only a single spur on each hind tibial apex, and none at all on the middle tibiae. Also, no known worker *Simopone* has the completely cut-through promesonotal suture of *C. annosus*.

Our archetype, then, is a form unknown to us from specimens, either fossil or living, but one likely to have been ancestral to *Simopone* as well as *Cerapachys*. These considerations raise the possibility that the archetypal *Cerapachys* may have had a more or less depressed, laterally marginate petiolar node, like those of *Simopone* and the "*Phracaces* lineage" of *Cerapachys*, but this is doubtful, because (a) there are differences in general structure between the *Phracaces* and *Simopone* petioles that may be important, and (b) the fossil species *annosus* and *faustus* show no signs of petiolar flattening or lateral margination.

It seems unlikely that *Sphinctomyrmex* gave rise to *Cerapachys*, since the *Sphinctomyrmex* characters are mostly reduction traits when compared to the likely *Cerapachys* archetype. The constrictions between gastric segments, reminding one of the rhagagistrine thynnine wasps, is most likely a derived character in *Sphinctomyrmex* and the allied genus *Leptanilloides*, but it doubtless goes back to the early part of the cerapachyine radiation, because *Leptanilloides* still has the deep-cut promesonotal suture in combination with it. It is also worthy of note that *Sphinctomyrmex* (and

*Leptanilloides* are in South America, while the flattened, marginate petiole ("*Phyracces*" and *Simopone*) is unknown in the New World, living or fossil. On the other hand, *Phyracces*-like species dominate Australia and have radiated exuberantly there, to the near exclusion of *Cerapachys*. Perhaps a thorough study of cerapachyine male terminalia, and of karyotypes, will help to clarify phylogeny in the genus and the tribe.

## Key to *Cerapachys* of Africa and the Middle East (Workers)

1. Antennae with 12 segments ..... 2  
Antennae with 11 segments ..... 13
2. Petiolar node with sharp dorsolateral margins (fig. 4) ..... 3  
Petiolar node without dorsolateral margins, the dorsal surface rounding evenly into the sides (fig. 3) ..... 8
3. Petiolar node seen from above forming 2 broadly rounded lobes behind, separated by a deep concavity (S Africa: Karroo) ..... *braunsi* [29]  
Petiolar node with angulate or dentate posterolateral corners, the posterior margin between them transverse, at most only gently concave ..... 4
4. Trunk coarsely longitudinally costulate its entire dorsal length; color black (C and W Africa) ..... *foerli* [27]  
Trunk dorsum smooth or punctate; longitudinal costulae, if present, confined to the anterior and posterior extremities of the surface ..... 5
5. Petiolar node much more closely and roughly sculptured and with much denser pubescence than trunk ..... 6  
Petiolar node and dorsum of trunk with similar sculpture and pubescence ..... 7
6. Eye length < apical antennomere L<sub>1</sub>, and eye separated from mandibular insertion by half or more of its maximum length; at least traces of costulation at anterior and posterior ends of trunk and on propodeal declivity; sculpture of petiole and postpetiole coarse and deep, often elongate (E S. Africa: Natal) ..... *vespula* [27]  
Eye larger, its maximum length > apical antennomere L<sub>1</sub>, only narrowly separated from mandibular insertion; trunk without traces of longitudinal striation, declivity smooth and shining; sculpture of petiole and postpetiole fine and superficial (Rhodesia) ..... *oxalis*
7. Larger species (petiolar node W > 0.50 mm), black; trunk, petiole, postpetiole, and gaster shining, with abundant, small but very distinct, round punctures, rather even in size and evenly distributed throughout (C Africa: Fernando Po I.) ..... *nkomoensis* [28]  
Smaller species (petiolar node W < 0.45 mm), ferruginous with piceous gaster; punctures finer, indistinct or not evenly distributed (Kenya) ..... *braytoni* [34]
8. Eyes absent or minute, at most with 1-2 pigmented facets (queens of these species are still unknown; they could be either winged or ergatoid, and if ergatoid, they may have large eyes, in which case they would probably key out as workers to 10) ..... 9  
Eyes large, with many (8 or more) facets ..... 10

9. Promesonotal suture distinct (Rhodesia to Cape Prov.) ..... *uerrugtoni* [32]  
Promesonotal suture obsolete (Kenya: Nairobi) ..... *kenyensis*
10. Petiolar node slightly but distinctly longer than broad (but ergatoid, if it occurs in this species, may have petiolar node broader!) (figs. 66-69; C Africa) ..... *centurio* n. sp. [31]  
Petiolar node broader than long ..... 11
11. Dorsal surface of head behind eyes very finely roughened and opaque over and between larger punctures (pronotum, petiole, and postpetiole with similar opaque sculpture; first gastric segment with very fine, dense punctation on a shining surface; color black; mts. of E Rhodesia) ..... *sylicicola*  
Dorsal surface of head behind eyes mostly smooth, or nearly so, with scattered punctures, though sometimes with a roughened area along the extreme posterior margin (sculpture of rest of body at least partly different from that described for *sylicicola*; color black to ferruginous) ..... 12
12. Petiole and postpetiole both with coarse, contiguous, and confluent punctures, overlain in large part by punctulate-granulose microsculpture that renders the surface prevailingly opaque (color dark reddish brown; Malawi; S Sudan) ..... *lambornii* [30]  
Petiole and postpetiole, or at least one of these segments, with separate punctures, the interspaces smooth and shining ..... remaining species of the *cribrimidis* group [30]
13. Eyes reduced, consisting of less than 15 facets in worker (Syria) ..... *puschardi*  
Eyes in worker larger, with well over 15 facets (C Africa) ..... *nitidulus*

## Preliminary Key to Indo-Australian *Cerapachys* (Workers and Ergatoid Queens)

Warning! New users should see notes on this key [23].

1. Antennae 12-merous ..... 2  
Antennae with (10 or) 11 segments ..... 71  
Antennae 9-merous ..... 75
2. Sculpture predominantly strongly costate over head and body (color black, figs. 48, 49); *crasyleyi* group ..... 3  
Sculpture predominantly punctate on a smooth or finely sculptured background, sometimes with only the petiole costate (rarely with trunk and gaster or postpetiole longitudinally striate, but in these cases the head and petiole are punctate or foveolate) ..... 4
3. Gaster (behind postpetiole) smooth, with numerous separated piligerous punctures (Taiwan) ..... *sauteri* [24]  
Gaster costate like head, trunk, petiole, and postpetiole (figs. 48, 49; Sumatra; Borneo; Philippines) ..... *crasyleyi* [24]
4. Petiole with strong overhanging dorsolateral margins (fig. 4) ..... 5  
Petiole with dorsum rounding into sides; dorsolateral margins absent or vestigial, or confused with the sculpture (figs. 3, 52, 63) ..... 46
5. Species from:  
Australia ..... 6  
New Guinea ..... 38  
New Caledonia ..... 39  
Oriental region ..... 40



6. Posterior corners of head on each side with a sharp dorso-lateral carina or margin curving toward eye (inset); color red, although gaster and petiole may be black or clouded with fuscous markings ..... 7  
Postocular carinae absent (fig. 4), or, if partly indicated, then the body color is black or nearly so ..... 14
7. Eyes very large, occupying about 1/3 of sides of head, and distinctly longer than space between eye and mandibular insertion; body size small, WL < 1.50 mm (SW Australia) ..... *varians* ..... 8  
Eyes occupying less than 1/3 of sides of head, their greatest diameter equal to or < distance between eye and mandibular insertion ..... 8
8. Postpetiole as long as, or slightly longer than, wide; humeral angles as seen from above very pronounced, subacute (Queensland) ..... *jovis* [38]  
Postpetiole wider than long; humeri rectangular or rounded as seen from above ..... 9
9. Propodeal dorsum rounded into declivity without an intervening transverse cariniform margin (color red, petiole and gaster sometimes infuscated) ..... 10  
Propodeal dorsum meeting declivity at a transverse cariniform margin (color red) ..... 11
10. Ocelli present and well developed (W Victoria) ..... *pictus* [38]  
Ocelli absent (Queensland to S Australia) ..... *singularis* [38]
11. Pronotal humeri as seen from above rectangular ..... 12  
Pronotal humeri as seen from above rounded ..... 13
12. Ocelli present:  
TL about 9 mm (Queensland) ..... *heros* ?  
TL about 7 mm (SW Australia) ..... *flammeus* ?  
Ocelli absent:  
TL about 9 mm; margin separating dorsum from declivity of propodeum fine, not very distinct in the middle; petiole as seen from above with distinctly concave anterior border, rectangular anterior corners, and broad, rounded lobiform posterior teeth (Queensland) ..... *heros* ?  
TL 6-8 mm; margin separating dorsum from declivity of propodeum strong and sharp; petiole with nearly straight (very feebly concave) anterior border and broadly rounded anterior corners; posterior teeth acute triangular (SW Australia) ..... *brevicollis* ?  
TL 6-7 mm (SW Australia) ..... *flammeus* ?  
TL 7.5-8 mm (NW Victoria) ..... *crassus* ?
13. TL about 6 mm; ocelli very small in type specimen (NW Australia) ..... *myobergi*  
TL > 9 mm; ocelli well developed in type specimen (S Australia) ..... *grandis*
14. With 3 well-developed ocelli; body red throughout (♀ ♀ and ergatoid queens) ..... 15

- Without developed ocelli in ♀, though one or more ocellar pits may be present (queens ergatoid with ocelli, or winged/dealate); color reddish, black, bicolored, or variegated ..... 20
15. Size rather small, TL 4-6 mm ..... 16  
Size larger, TL 7-10 mm ..... 17
16. Postpetiolar node as long as or slightly longer than wide, with nearly straight sides diverging caudad; very slender species (TL about 4.4 mm), probably based on ergatoid queen (SW Australia) ..... *angustatus*  
Postpetiolar node distinctly wider than long, with rounded sides; posterior coxa without lamina; TL 5.5-6 mm (SW Australia) ..... *greavesi*  
(N Victoria) ..... *macrops*
17. Propodeal declivity with distinct lateral margins extending halfway or more down the sides ..... 18  
Propodeal declivity without distinct lateral margins, except for a very short, indistinct spur at upper corner on each side ..... 19
18. Head in full-face view with posterior border straight or convex, the corners rounded; TL 8-8.5 mm:  
(NW Victoria) ..... *gwynethae*  
(SE Queensland) ..... *pliventris*  
Head in full-face view with posterior border distinctly concave, the corners sharply angulate; TL presumed ergatoid queen 7.4 mm (SW Australia) ..... *constrictus*
19. Postpetiole with a strong, straight, carinate transverse anterior margin that joins the sides at definite angles; ♀ and alate ♀ TL 8-10 mm (W & S Australia to N Queensland) ..... *principes* [39]  
Petiole without a distinctly carinate anterior margin; anterior corners as seen from above rounded; ♀ TL about 8 mm (ergatoid ♀ of *C. potteri* 9-10 mm):  
(WC & NW Australia) ..... *systedti*  
(N Victoria) ..... *potteri*
20. Pronotum and propodeum dorsolaterally marginate ..... 21  
Pronotum and propodeum immarginate laterally, the dorsum rounding into the sides ..... 37
21. Head, trunk, petiole and postpetiole black ..... 22  
At least the head or petiole yellow or red ..... 26
22. Gaster (after postpetiole) all red (SE Australia, forest) ..... *fuscus*  
Gaster black or piceous ..... 23
23. Petiole, postpetiole, and gaster with dense, fine, appressed and decumbent, gray pubescence (SE Australia, savanna and savanna woodland) ..... *senescens*  
Petiole, postpetiole, and gaster with dorsal reclinate pubescence virtually lacking, or at most very dilute ..... 24
24. Petiolar node almost exactly as wide, and nearly the same length, as postpetiole (N Queensland) ..... *binodis* [48]  
Petiolar node notably narrower than postpetiole, or much shorter, or both ..... 25
25. Disc of petiolar node distinctly more than 3/4 as long as wide (including posterior teeth or angles); sides strongly convex and posterior teeth well developed and directed caudad (SE Australia, forest) ..... *larvatus*  
Disc of petiolar node short and wide, L only about 3/4 W; sides



- straight or weakly convex; posterior teeth subrectangular or short and blunt [46]:  
(Queensland) ..... *turneri*  
(Queensland) ..... *adamus*  
(SE & SW Australia) ..... *nificornis*
26. Body colorous red or yellowish ..... 27  
Body bicolor, or variegated ..... 33
27. Posterior corner of petiolar node armed with sharp, projecting angles or strong teeth ..... 28  
Petiolar node rounded behind, or else without more than obtuse vestiges of teeth on receding posterolateral corners ..... 32
28. Small species (♀ TL 3.3-5 mm, dealate ♀ TL 3.4-4 mm) with very large eyes about twice as long as the distance between eye and mandibular insertion, and taking up ½ or more of the sides of the head (SW Australia) ..... *incentatus* [43]  
Larger species (♀ TL > 3.5 mm); eyes at most only slightly longer than the anteocular space, and not taking up more than about ¼ of the sides of the head ..... 29
29. Petiolar teeth as seen from above directed caudad and usually curved a little inward (mesad), so that their apices do not extend out past anterior corners of postpetiole ..... 30  
Petiolar teeth as seen from above acutely triangular and directed obliquely outward (laterad) so that they project a little beyond anterior corners of postpetiole ..... 31
30. Petiole node (excluding posterior teeth) considerably less than twice as wide as long; center of clypeal declivity with only a minute tubercle or carina; ♀ TL 4.2 to perhaps 6 mm (N Queensland to SW Australia) ..... *feroidus* [42]  
Petiole node (excluding teeth) about "twice as broad as long;" middle of clypeus "with a long tooth-like projection," ♀ TL "3.5-4 mm." *vide* Clark (SW Australia) ..... *latus*
31. Postpetiole subquadrate, about as wide as long, or only slightly wider, with nearly straight sides; the lateral margins broad and often notched at the abruptly rounded anterior corners, but fine and disappearing gradually along the posterior half of the sides (SW Australia) ..... *punctatissimus* [44]  
Postpetiole markedly broader than long, with broadly rounded anterior corners and convex sides, each bearing a lamella that ends abruptly in a low, blunt angle behind the mid-length (SW Australia E to dry inland of SE Australia and N to Darwin) ..... *clarki* [44]
32. Petiole as seen from above broadly rounded behind, without traces of angles; posterior border may be very feebly concave mesad; ♀ TL 4.4-4 mm; ergatoid ♀ TL 4.8 mm (SW Australia) ..... *simmonsae*  
Petiole as seen from above with posterior half suddenly narrowed, the sides sharply converging; posterior teeth reduced to very small, obtuse vestiges; ♀ TL about 5 mm (SW Australia) ..... *picipes*
33. Petiolar node predominantly dark brown discal, like the adjacent propodeum and postpetiole; ♀ TL 3.4-3.8 mm, ergatoid ♀ TL about 5 mm (SW Australia) ..... *gilesi*  
Petiolar node with a yellow or light reddish disc ..... 34
34. Eyes more than ½ as long as sides of head and about twice as long as eye to nearest part of mandibular insertion ..... 35  
Eyes less than ½ of sides of head and subequal in length to the distance from eye to mandibular insertion ..... 36
35. Petiole yellow, postpetiole predominantly contrasting brown or black; trunk and/or head varying, brownish yellow to brown; ♀ TL 3.2-3.4 mm (W & C Australia) ..... *brevis* [49]  
Head, trunk, petiole, and postpetiole yellowish red; remainder of gaster black or brown; ♀ TL 2.9-3.2 mm (SW Australia) ..... *nigricornis*
36. Anteocular space completely bounded above (dorsomesad) and below (ventrolateral) by 2 distinct carinae that reach the eye; trunk, postpetiole, and gaster dark brown, head reddish; ♀ TL 5.3-5.6 mm (SW Australia) ..... *bicolor*  
Anteocular space open; dorsomesad carina not reaching the mesal margin of the eye, and ventrolateral carina absent except for a very short spur at the mandibular insertion; head and petiole red or yellow, postpetiole and gaster dark brown or black, trunk red or yellow with varying infuscation and sometimes almost completely brown; TL 3.7-4 mm, dealate TL 5.4-5.6 mm (E New South Wales) ..... *elegans*
37. Head, trunk, petiole, postpetiole, and gaster black (N Queensland) ..... *aberrans* [47]  
Head and trunk red or brown, trunk and petiole red, gaster black or dark brown (Queensland W to Darwin and vic.) ..... *longitarsus* [33]
38. Body black; small species, pronotal W < 0.52 mm (rain forest) ..... *marginatus*  
Head, trunk, and petiole red, gaster black; larger species, pronotal W > 0.55 mm ..... *krombeini*
39. Large species (HW > 1.1 mm) with long scapes reaching nearly to posterior corners of head in full-face view; dorsal surface of trunk rounding smoothly into sides ..... *dumbletoni*  
Smaller species (HW < 1.1 mm); scapes reaching only a little way past eyes in full-face view; pronotum and propodeum with distinct lateral margins ..... *cohici*
40. Large black species, postpetiole > 0.80 mm long; very densely and evenly punctate, and body with fairly numerous long, curved, fine hairs, but dorsal surfaces without appreciable pubescence (Malaya; Borneo; Philippines; Celebes) ..... *puscillatus* [50]  
Postpetiole L < 0.80 mm, its dorsal surface with distinct, often fairly dense, appressed and decumbent pubescence usually extending to gaster and other parts of the body ..... 41
41. Ventrolateral margins of the head sharply carinate and continuous from posterior corners of head to mandibular insertions; black (fading to dark brown?) species with postpetiole wider than long (Borneo) ..... *heurtitzi* [51]  
Ventrolateral margins of the head distinct only in the posterior part of the head, and sometimes for a short distance back from mandibular insertions, obliterated or indistinct or reduced to a line of punctures over a wide middle area; color not black, or, if black, then postpetiole is as long as, or longer than, wide ..... 42
42. "Head coarsely rugose" (Basilian I.) ..... *bakeri* [60]  
Head not rugose ..... 43
43. Eyes situated only about half their greatest diameter distant from mandibular insertions ..... 44  
Eyes situated about their own length, slightly more or less, distant from mandibular insertions ..... 45

44. Dorsal surfaces of body shining, but regularly and rather densely sown with small punctures; pilosity consisting mostly of short, fine, appressed and decumbent, pubescent-like hairs, abundant on trunk, petiole, and gaster as well as on postpetiole; longer standing hairs very sparse or absent over most of body; color uniform brown (Philippines) : *lucuriae*  
Dorsal surfaces of body shining, with widely scattered, mostly indistinct, small punctures and many generally distributed standing hairs, only the postpetiole densely punctulate and appreciably pubescent; head brown, trunk red or brown, petiole and postpetiole light to dark reddish, gaster brown or black (widespread) : *longitarsis* [33]
45. Postpetiole longer than broad, dorsum of propodeum rounded into declivity without a transverse carina; body black, with many, generally distributed, long standing hairs in addition to appressed pubescence (Borneo; Sumatra) : *pubescens* [51]  
Postpetiole a little wider than long; dorsum of propodeum separated from declivity by a delicate transverse carina; head, trunk, petiole, and postpetiole dull brownish-yellow, gaster darker brown; pilosity limited almost completely to a copious decumbent pubescence, with only a few long standing hairs on head and gastric apex (SE Asia) : *singaporensis*
46. Dorsal surface of petiolar node with a smooth, median, longitudinal groove or smooth, flat median area (*antennatus* group) [25] : 47  
Dorsal surface of petiolar node rounded and punctate, without a differentiated median groove or smooth area : 49
47. Antecular space (cheek) crossed by 1 or more longitudinal grooves or a connected chain of punctures running from eye to border of mandibular insertion; petiolar disc costate or smooth : 48  
Antecular space smooth, without such a groove, and with only scattered punctures; petiolar disc with at least 4 strong longitudinal costae, the median interspace narrow, in both ♂ and ♀ (Greater Sunda Is.; Malaya; Philippines) : *jacobseni* [25]
48. Workers and small queens with costate petiolar disc; larger ergatoid and larger perfect queens with costae weak or absent, disc wide, with broad, median, smooth strip; Workers, small queens, ergatoids (S China: Himalayas; SE Asia; Sunda Is. to Philippines) : *salzinodis*  
Large perfect queens (Sumatra; Borneo) : *manni*  
Worker with smooth petiolar disc (N Borneo) : *antennatus*
49. Species from Indo-Malayan region : 50  
Species from Melanesia (adapted in part from Wilson 1959: 44-45) : 59
50. Dorsal surfaces of body very densely and finely punctulate and finely pubescent (pruinose or subpruinose), virtually without longer standing hairs; sides of petiole with a fine vestigial dorsolateral margin, visible only in certain lights and views; color blackish brown (figs. 51-53; Philippines: Negros I.) : *pruinosus*  
Dorsal surfaces of body either prevailing smooth and shining, with spaced punctures or else with larger, crowded foveolae; standing hairs generally distributed and usually abundant : 51
51. Punctures on dorsum of head relatively small, separated, their diameter smaller than the average distance separating them : 52
- Punctures on dorsum of head large, foveiform, crowded, their diameter as large as, or larger than, the average distance separating them, and in some cases they are contiguous (figs. 60, 61) : 55
52. Declivity of propodeum with distinct cariniform margins, continuous across the top; punctures of head fairly coarse, a few of them separated by less than a diameter (Sarawak) : *bryanti* [55]  
Declivity of propodeum with indistinct margins, especially across the top; head punctures small, usually all separated by more than a diameter (fig. 54) : 53
53. Petiolar node as seen from the side distinctly higher than long (excluding subpetiolar process), with dorsal surface rising to a rather narrowly rounded summit in the posterior half (fig. 56; Ceylon) : *lateoviger*  
Petiolar node (excluding subpetiolar process) as long as, or longer than, high; summit gently rounded, the highest point near midlength : 54
54. Petiole and postpetiole with rather dense, shallow punctate-rugulose sculpture and densely covered with subdecumbent hairs and pubescence; body red or bicolored (Philippines: Negros I.) : *rugiflorax*  
Petiole and postpetiole smooth and shining, with scattered coarse punctures and only sparse decumbent and subdecumbent pilosity (Philippines) : *muiri*
55. Propodeal declivity without a distinct, complete margin, at least at the top (*vide* Viehmeyer); postpetiole with fine longitudinal striation superimposed on dense, shallow foveolation; gastric dorsum very densely punctate and probably densely pubescent in undamaged specimens (Celebes, in copal) : *conservatus*  
Propodeum bounded by a distinct carinate margin above and laterally; postpetiole without fine longitudinal striation : 56
56. Petiolar node seen from above longer than wide and coarsely, densely foveolate (figs. 59, 63, peninsular India) : *indicus*  
Petiolar node as wide as, or wider than, long : 57
57. Head reddish brown or red; trunk and both nodes red; gaster black or dark brown (India) : *aikteni*  
Body unicolorous yellowish, red, brown, or black : 58
58. Reddish yellow *vide* Emery (known only from winged queen; Taiwan) : *reticulatus*  
Red to reddish brown (Borneo; Sumatra) : *doherthy* [53]  
Dark brown *vide* Karavaiev (Java) : *salimani*
59. Species of Western Melanesia: New Guinea, Bismark Archipelago, Solomons, etc. : 60  
Species of Fiji Islands : 67
60. Dorsa of trunk and first gastric segment entirely covered by dense longitudinal striation (N New Guinea) : *opacus*  
Dorsa of trunk and first gastric segment lacking striation : 61
61. Dorsa of postpetiole and gaster densely and finely punctate and subopaque, the pilosity at least as dense as that of appendages and predominantly appressed-subappressed (Papua) : *desposyne*  
Dorsa of postpetiole and gaster at most bearing scattered foveolae or punctures, their surfaces shining; pilosity of these sclerites notably less dense than that of appendages, predominantly erect-suberect : 62

62. Head roughly sculptured, rugose-reticulate to contiguously foveate; larger species, HW including eyes  $> 0.89$  mm (N New Guinea) ..... *superatus*
- Head relatively smooth, at most bearing separated foveolae or punctures; smaller species, HW including eyes  $< 0.80$  mm ..... 63
63. Sides of petiolar tergum shagreened and opaque to subopaque, densely clothed with short, appressed-subappressed, grayish hairs, thus contrasting with sides of postpetiolar tergum, which are smooth and shining and bear predominantly standing pilosity no denser than that on sides of adjacent gastric tergite I (N New Guinea) ..... *polynikes*
- Sides of petiolar and postpetiolar terga variable, but the surfaces of the 2 terga do not contrast with each other as described above ..... 64
64. Dorsum of head with coarse umbilicate foveolae, many of them contiguous or subcontiguous (N New Guinea) ..... *inconspicua* [52]
- Dorsum of head smooth, with small, separated punctures ..... 65
65. Head of unique type specimen only 0.36 mm wide (N New Guinea) ..... *dominitus* [52]
- Head  $> 0.45$  mm wide ..... 66
66. Head punctures very fine (New Guinea) ..... *flavoclavata* [52]
- Head punctures coarser (Solomons) ..... *terricola* [52]
67. Dorsum of postpetiole covered by foveolae about 0.03 mm in diameter and separated by interspaces of about the same magnitude; smaller species, HW  $< 0.67$  mm ..... 68
- Dorsum of postpetiole smooth and shining, at most with scattered, fine punctures; larger species, HW ordinarily  $> 0.70$  mm, and less than this only in occasional nanitic workers ..... 69
68. Entire truncal dorsum covered with abundant foveolae about 0.03 mm in diameter ..... *sculpturatus*
- Most of central portion of truncal dorsum smooth and shining ..... *vitensis*
69. Lateral surface of petiole covered by contiguous foveolae about 0.06 mm in diameter; petiole (including peduncles) distinctly wider than long ..... *majorculus*
- Lateral surface of petiole bearing only scattered, fine punctures, most of its area smooth and shining; petiole (including peduncles) distinctly longer than wide ..... 70
70. Sterna of petiole and postpetiole completely covered by subcontiguous foveolae about 0.06 mm in diameter ..... *lindrothi*
- Sterna of petiole and postpetiole lacking foveolae, with surfaces almost completely smooth and shining ..... *zimmermani*
71. Eyes large in worker and queen, greatest diameter  $>$  maximum width of anterior tibia; body shining, sown with coarse umbilicate foveolae, but with broad, smooth, and shining interspaces on trunk (figs. 75, 76, 78) ..... 72
- Eyes in workers and ergatoid queens small to absent; if present, their greatest diameter  $<$  maximum width of anterior tibia; head, trunk, and nodes opaque to subopaque, very densely, evenly, and contiguously covered with small punctures (figs. 79–84) ..... 73
72. Body bicolored; head, trunk, and nodes brownish red (head infuscated), gaster black or dark brown (Ceylon) ..... *fissulatus* [59]
- Body unicolorous dark reddish brown (Kalimantan) *kodocorum* [58]
73. Worker and ergatoid queen small and slender, HW  $< 0.50$  mm; petiolar and postpetiolar nodes both longer than wide (Ceylon) ..... *fragans* [65]
- Size larger, more robust, HW  $> 0.50$  mm; petiolar and postpetiolar nodes as wide as, or wider than, long ..... 74
74. Larger species, HW  $> 0.65$  mm; eyes always distinct and multifaceted (fig. 79) in worker and ergatoid queen (S India) ..... *betucheti* [64]
- Smaller species, HW  $< 0.65$  mm; eyes of worker absent or reduced to a single indistinct facet and an obscure pigment spot (Ceylon) ..... *coccus* [65]
75. Size larger; worker HW  $> 0.70$  mm; (Fiji Is.) ..... 76
- Size smaller, worker HW  $< 0.60$  mm ..... 77
76. Foveolae of central part of postpetiolar dorsum indistinct, mostly  $< 0.02$  mm in diameter; color pale reddish brown (Fiji Is.: Viti Levu) ..... *cryptus*
- Foveolae of central part of postpetiolar dorsum distinct, mostly  $> 0.02$  mm in diameter; color dark reddish brown (Taveuni) ..... *fuscior*
77. Postpetiole more than half as long as the succeeding (first gastric) segment; head long and narrow, CI about 70; surface of head and truncal dorsum finely roughened between punctures, opaque (Ceylon) ..... *typhlus* [65]
- Postpetiole less than half as long as first gastric segment; head wider, CI  $> 73$ ; surface between punctures of truncal dorsum, and often of head, mostly smooth and shining (when clean), even if very narrow ..... 78
78. Anterolateral shoulders of first gastric segment as seen from above broadly rounded and gradually widening caudad (fig. 95) ..... 79
- Anterolateral shoulders of first gastric segment as seen from above abruptly rounded, accentuating the medium concavity that receives the postpetiole ..... 80
79. Head nearly as broad as long, HW usually 0.50–0.56 mm; punctures on dorsum of head mostly separated by smooth, shining interspaces averaging as wide as, or wider than, the puncture diameter (tropical and subtropical Australia) ..... *edentatus* [61]
- Head narrower, HW usually 0.40–0.48; punctures on dorsum of head crowded, mostly contiguous or nearly so (China; India; SE Asia, introduced in Hawaii and the West Indies) ..... *biroi* [63]
80. Postpetiole longer than broad (fide Mann; Solomons: Ugi I.) ..... *pavea* [62]
- Postpetiole as wide as, or wider than, long (New Guinea) ..... 81
81. Head with spaces between punctures finely sculptured, subopaque; postpetiole distinctly broader than long (New Guinea) ..... *papuanus* [62]
- Head smoother and more shining between punctures; postpetiole almost as long as broad (New Guinea) ..... *pusillus* [62]

## Preliminary Partial Key to New World *Cerapachys* – (Workers)

1. Antennae 12-merous (Trinidad) ..... *neotropicus*
- Antennae 11-merous ..... 2

Antennae 9-merous (Trinidad; Puerto Rico; introduced from Asia) ..... *birui* [63]

2. Body smooth and shining, with widely spaced punctures (SE Brasil) ..... *splendens*  
Body densely sown with coarse foveolae or punctures, mostly contiguous on dorsum of head (N and C America) .....  
..... *augustae* group [66]  
(Texas to Arizona, N Mexico) ..... *augustae*  
(Guatemala; Belize, etc.) ..... *toltecus*  
(Honduras) ..... *hondurians*  
(Males taken at light in Texas, New Mexico, and Arizona are referred to *C. augustae* and *C. davisi*.)

## Sphinctomyrmex

- > *Sphinctomyrmex* Mayr, 1866:895, ♀. Type: *Sphinctomyrmex stali*, 1866, monobasic. —Borgmeier, 1957:104, ♀, discussion of *S. stali*.
- > *Cerapachys* Forel, 1893:461, not F. Smith.
- > *Eusphinctus* Emery, 1893, Ann. Soc. Entomol. France, 61 (1892): cclxxx, ♀. Type: *Eusphinctus furcatus*, 1893, by original designation, monobasic. —1895a:pl. 14, fig. 4, ♂ genitalia.
- > *Sphinctomyrmex* subgenus *Eusphinctus*: Emery, 1894b:457. —1911:7, ♀, species list.
- > *Eusphinctus*: Wheeler, 1918:219, 224, review of Australian spp. with key.
- > *Eusphinctus* subgenus *Eusphinctus*: Wheeler, 1918:219, diagnosis; 224-231, review of Australian spp. with key.
- > *Eusphinctus* subgenus *Zasphinctus* Wheeler, 1918:219, 233. Type: *Eusphinctus* (*Zasphinctus*) *turneri* Forel, monobasic.
- > *Eusphinctus* subgenus *Nothosphinctus* Wheeler, 1918:219, 225, 233-239, diagnosis and review of Australian spp. with key. Type: *Sphinctomyrmex froggatti* Forel, by designation of Donisthorpe, 1943, Ann. Mag. Natur. Hist., (11)10:675.
- > *Aethiopsopone* Santschi, 1930:49, ♂. Type: *Sphinctomyrmex rufoventris* Santschi, monobasic.

**Worker:** With characters of *Cerapachys*, but gastric segments IV, V, and VI separated by distinct constrictions and (except for *S. furcatus* and *S. taylori*) nearly equal in length. Eyes reduced to very small size or altogether lacking (except in *S. turneri*, which has fairly large, convex eyes). Antennae with 11 or 12 segments; palpi usually segmented 3,3. Sculpture of round piligerous foveolae, sparse or crowded, with smooth or finely roughened interspaces. Hairs short, simple, sparse to fairly dense; pubescence sometimes present on petiole, postpetiole, or succeeding gastric segments. Color black, brown, red, or yellow.

**Queen:** A morphocline ranges from perfect winged (or dealate) females with large eyes, ocelli, etc., to blind subdichthadiiform queens that are workerlike except for larger size and broader head and petiole, and sometimes vestigial eyes and 1 ocellus. Intermediates exist in, e.g., *S. steinheili* and *S. asper*; these may have compound eyes of modest size and 3 ocelli, but workerlike trunk. It seems likely that the species with subdichthadiiform queens have monogynous colonies, while at least some of the dealate or intermediate forms are found several (to more than 20) to a single colony. It is not known whether the multiple queens are all functional reproductives.

**Male:** Differs from *Cerapachys* male by the distinctly

constricted subequal segments of the gaster, and even here a difficulty exists because some American *Cerapachys* have narrowed bases to the main gastric segments. The male of *S. furcatus*, like its worker, has the gastric segments unequal, with the first much the largest. Antennal segments 13, rarely (*S. furcatus*) 12.

Aside from *S. furcatus*, males of *Sphinctomyrmex* divide into 2 classes. The first class, associated in a few cases with workers and/or queens (*S. steinheili*, *S. turneri*, *S. asper*) has slender males with triangular mandibles, and usually distinct notauli. The second class, consisting of males taken at light, probably belongs with the species having subdichthadiiform queens (*froggatti* group); these have long, tapered, falcate mandibles and lack distinct notauli; they tend to be larger and relatively robust, and have denser, softer, more regularly arranged pilosity, particularly on head and mandibles (figs. 97, 98); see also fuller discussion at [67].

The genus *Sphinctomyrmex* was first described by Mayr (1866:895) from a single dealate queen with 12-segmented antennae (*S. stali*) from southeastern Brasil. Although at least one winged queen of *Sphinctomyrmex* had already been collected in West Africa in the last century [70], the genus was not to be reported in print from that continent again until Santschi's record of 1915. Forel described forms from Australia (as *Cerapachys*) in 1893 and 1895, and in 1895 Emery introduced the new generic name *Eusphinctus* for a worker from Burma with 11-segmented antennae that he named *E. furcatus*. New *Eusphinctus* species were added from New Guinea by Emery (1897) and from India and Australia by Forel, who both saw that workers of some species had 11, others 12, antennal segments, and therefore regarded *Eusphinctus* only as a subgenus of *Sphinctomyrmex*. André (1905) noted that the Indo-Australian species known at the time differed from the lone neotropical species, *S. stali*, in that they had ergatoid queens, whereas the *S. stali* queen had well-developed thoracic sclerites and had obviously once borne wings. On this basis, he recommended that *Sphinctomyrmex* and *Eusphinctus* be recognized as separate genera. Emery, in his 1911 ponerine fascicle of the Genera Insectorum, kept *Eusphinctus* at subgeneric level. In 1918, however, Wheeler not only embraced André's generic separation, but went on to subdivide *Eusphinctus* into 3 subgenera:

1. *Eusphinctus* s. str. Workers and females with 11-jointed antennae, with entire or emarginate pygidium, the workers blind, the females with eyes and ocelli. Habits hypogaeic.
2. *Nothosphinctus* subgen. nov. Workers and females with 12-jointed antennae; the former blind and with entire pygidium, the latter with emarginate pygidium and either blind or with very minute eyes and the anterior ocelli. Habits hypogaeic.
3. *Zasphinctus* subgen. nov. Workers large, dark colored, with 12-jointed antennae and well developed eyes, but without ocelli. Females unknown. Habits probably epigaeic.

Meanwhile, Santschi (1915) had described a species of *Sphinctomyrmex* from males taken at light in West Africa. Wheeler (1918) dismissed Santschi's generic assignment as

"open to doubt." But when Santschi read Wheeler's 1918 revision, he displayed his carefree notion of generic-level taxonomy by making *S. rufiventris* the type of a new genus, *Aethiopopone*, and justified his action as follows (Santschi

En 1915, quand je décris cette espèce en la rapportant au genre *Sphinctomyrmex*, l'habitat de celui-ci était considéré comme étant le Brésil, l'Australie et l'Inde, et le 3<sup>e</sup> était encore inconnu. Or, le  $\delta$  de *S. rufiventris* avec ses caractères de *Proderulinus*, surtout ses segments abdominaux étranglés, son habitat intermédiaire, me fit risquer une identification pareille à celle que firent Forel et Emery en rapportant à ce genre les *Eusphinctus* du vieux monde. Ce n'est du reste qu'en 1918 que Wheeler fit la distinction générique, ne considérant plus que comme *Sphinctomyrmex* la ♀ *S. stali* Mayr du Brésil. En élevant au rang de genre le sous-genre *Eusphinctus* Em. pour les espèces indo-australienne, il le divise en trois sous-genres: *Eusphinctus*, *Nothosphinctus* et *Zasphinctus*. Cela étant donné, je me vois obligé de créer un nouveau genre pour l'espèce africaine. Les caractères de celle-ci tiennent des *G. Sphinctomyrmex*, *Cerapachys* et *Sinopone*.

This house of cards should have been fluttered away in 1923 by Clark when he described *Eusphinctus occidentalis* from Western Australia. This species turned out to have a dealate queen with 11-segmented antennae associated with blind workers much like those of the eastern Australian *E. steinheili* and *E. duchsauzoyi*.

Further discoveries were the worker caste of *S. stali* (Borgmeier, 1957) [69] and the winged *Sphinctomyrmex* queen collected long ago by Afzelius in West Africa [70], already mentioned above, and also workers of *Sphinctomyrmex* dug out of the Ivorian savanna by Jean Lévieux [70]. Now another species has been found by Gotwald in rotting wood in Gabon (unpublished).

It seems from a survey of all the old and new material that we are dealing with a single genus in which the functional queens vary, according to species, from "normal" winged (when virgin) to ergatoid or even dichthadiiform types. This arrangement has already been tacitly accepted by Wilson (1957), and it would be well to deal with the diagnostic characters (Wheeler, 1918:219) one at a time.

**Specialization of queen.** The most primitive kind of queen (Africa, Brasil, Western Australia) has wings that are lost, presumably in the usual fashion, before the colony is founded, or at least before the queen joins an established colony. Queens of species such as *S. steinheili*, *S. asper*, and *S. duchsauzoyi* are wingless and ergatoid in thoracic structure, but have 3 distinct ocelli and a pair of compound eyes. In *imbecilis*, the queen has undergone further specialization; the head is broadened and its sides rounded, the ocelli are reduced to one, and the compound eyes are reduced to minute vestiges; this ant is clearly on its way towards becoming a dichthadiiform, and it is important to note that the development of wings and pterothorax is not the only criterion on which the queens may be sorted.

**Habits "hypogaecic" vs. "probably epigaecic."** Wheeler's use of this ethological character, even as stated, is obviously speculative. The meager evidence available fails to support his classification. I found *S. steinheili* travelling aboveground in full daylight during a raid on a nest of *Stigmacerus* in

Victoria, Australia, although the raiders used cracks in the soil for some parts of their trail (Wilson, 1958:136). On the other hand, I collected a worker of *S. turneri* foraging under leaves in dark rain forest in northern Queensland. At the very least, the distinction between these two species and their respective subgenera on hypogaecic vs. epigaecic foraging habits must be considered as blurred. In fact, Wheeler's classification is based on the presence or absence of worker eyes, a trait that may no more reflect foraging habits than it does in the true army ants. By the same token, it is possible, even probable, that some of the species with blind workers really are hypogaecic in foraging habits.

**Antennae 12-merous vs. 11-merous in worker and queen.** This character was weak to begin with, because the workers of forms with winged/dealate queens can have either 12 or 11 segments. *S. furcatus*, though not very close to the Australian "*Eusphinctus s. str.*," has 11 segments in worker and queen. Now we have *S. asper*, which is very close to the Australian *Eusphinctus s. str.* but has 12 antennal segments instead of 11. As in *Cerapachys*, antennal segment number apparently has undergone independent reductions that make it a poor group character.

**Pygidium notched vs. entire.** Wheeler (1918:219) noted that:

the worker of *E. cribratus* Emery of New Guinea has an entire pygidium and belongs with the Australian species in *Eusphinctus s. str.*, but the workers of the Indian species *E. furcatus* Emery and *taylori* Forel have a notched pygidium. Should future investigation show that the pygidial characters are correlated with other peculiarities or with different types of female, it may be advisable to restrict the subgenus *Eusphinctus* to the two Indian species and to suggest a new subgeneric name for the Australian and Papuan forms with 11-jointed antennae.

The emarginate pygidium itself is not a very impressive group character, since it is partly linked to size. "*Zasphinctus*" *turneri* has it in the worker, and "*Nothosphinctus*" queens have it, while workers do not. Also, emargination occurs to different degrees among the species that have it, and even the angle of view affects its distinctiveness.

The Indian species *furcatus* [68] has now been found to possess an ergatoid female with eyes modestly larger than the minute ones of its worker, although its overall body size hardly differs from that of the worker in the same colony. The differences in the proportions of the gastric segments between *furcatus* (fig. 100) and other *Sphinctomyrmex* seem not to have attracted much notice, though they weaken the separation between *Sphinctomyrmex* and *Cerapachys*. Now that we have the presumed males of *furcatus*, we note another difference in that this specimen has only 12 antennal segments, whereas all other known *cerapachyine* males have 13. The *furcatus* male also has the gastric segments proportioned about the same as in the worker, and its terminalia are fairly distinctive (although terminalia for related species are poorly known).

Forgetting about the emarginate pygidium, then, we might still make a fair case for separating *furcatus* and *taylori* into a genus *Eusphinctus* apart from both *Sphincto-*

*myrmex* and *Cerapachys*, but it seems unwise to do this in a group so poorly known as *Sphinctomyrmex*, in which males have yet to be matched up to workers or queens in most species, and in which many species doubtless remain undescribed from any caste. It seems that problems in this group will best be solved by rearing live colonies to get the males in association with the female castes.

**BIONOMICS:** Discussed previously under the tribe.

**DISTRIBUTION:** *Sphinctomyrmex* is best represented in numbers of species, and is decidedly more common, in Australia than in other parts of the world, but the genus also occurs in New Guinea, New Caledonia, and southern Asia.

At least 2, and probably more, species exist in west and central Africa, where the 2 were originally described from males, and 2 distinctly different, undescribed species are known in the worker caste, plus 1 undescribed form known from a winged queen. Elsewhere, *Sphinctomyrmex* is represented only by a single rare species from southeastern Brazil.

### SPHINCTOMYRMEX species

New combinations (authors' names in parentheses) formerly *Eusphinctus*.

- (T) *asper* Brown n.sp. ♀ ♂ N Queensland [73]  
 (T) *brunnicornis* (Clark) = *imbecilis*  
 (T) *caledonicus* Wilson 1957:8 ♀ ♂ New Caledonia  
 (?) *cedaris* Forel 1915:16 ♀ ♂ N Queensland [74]  
*chariensis* Santschi 1915:245 ♂ W Africa  
 (T) *clarus* (Forel) 1893:462 ♀ Australia: Adelaide R.  
*crinitus* (Emery) 1897:594 ♀ N New Guinea  
 (T) *duchaussoyi* André 1909:205 ♀ ♂ Australia: E coast [75]  
 = *hackeri* (Wheeler) 1918:229 ♀ ♂ n. syn.  
 (T) *emeryi* (Forel) = *perstictus*  
 (T) *fallax* Forel = *steinheili*  
 (T) *froggatti* Forel 1900a:71 ♀ E Australia [71]  
 (T) *fulvidus* (Clark) = *imbecilis*  
 (T) *fulvipes* (Clark) = *steinheili*  
 (T) *furcatus* Emery 1894:457 ♀ India; Burma [68]  
 (T) *hedwigae* Forel = *steinheili*  
 (T) *hirsutus* (Clark) = *steinheili*  
 (T) *imbecilis* Forel 1907c:272 ♀ ♂ SW & SE Australia [71]  
 = *manni* (Wheeler) 1918:236 ♀ ♂ n. syn.  
 = *fulvidus* (Clark) 1923:75 ♀ ♂ larva n. syn.  
 = *silaceus* (Clark) 1923:77 ♀ n. syn.  
 = *brunnicornis* (Clark) 1930:2 ♀ n. syn.  
 (T) *manni* (Wheeler) = *imbecilis*  
 (T) *myobergi* Forel 1915:16 ♀ SE Queensland  
 (T) *myops* Forel 1895c:421 ♀ (recte ♀) Queensland  
*nigricans* (Clark) 1926:44 ♀ NE New South Wales  
 (T) *occidentalis* (Clark) 1923:74 ♀ ♂ larva SW Australia  
 (T) *perstictus* Brown n. n. for *emeryi* (Forel) 1893  
 = *emeryi* (Forel) 1893:461 ♀ preocc. in *Cerapachys*  
 (T) *ryuiventris* Santschi 1915:244 ♂ W Africa (interior)  
 (T) *septentrionalis* (Crawley) 1925:577 ♀ Australia: Darwin dist.  
 (T) *silaceus* (Clark) = *imbecilis*  
 (T) *stali* Mayr 1866:895 ♀ SE Brazil [65]  
 (T) *steinheili* Forel 1900a:72 ♀ (recte ♀) E & SE Australia [74]  
 = *fallax* Forel 1900a:73 ♀ (Syn. Wheeler, 1918:225)  
 = *hedwigae* Forel 1910a:21 ♀ ♂ n. syn.  
 = *hirsutus* (Clark) 1929:118 ♀ ♂ n. syn.  
 = *fulvipes* (Clark) 1934b:49 ♀ ♂ n. syn.

- (T) *taylori* Forel 1900b:328 ♀ India [68]  
 (T) *trux* Brown n. sp. ♀ ♂ N Queensland [72]  
 (T) *turneri* Forel 1900a:70 ♀ E Queensland

### Species Groups

Owing to the fact that many males and queens remain unknown or unmatched with their workers, and also to the certainty that more species remain to be described, it is not yet possible to assort the *Sphinctomyrmex* species into firm groupings. A beginning can be made in this direction, however, and a grouping may be useful so long as it is accepted as tentative and incomplete.

Group of *stali*, neotropical: *stali*. Group of *ryuiventris*, tropical Africa: *ryuiventris*, *chariensis* (males), plus at least 3 species based on workers or queens. Group of *furcatus*, south Asia: *furcatus*, *taylori*. Group of *froggatti*, Australia: *clarus*, *froggatti*, *imbecilis*, *myobergi*, *trux*, *myops*, *nigricans*, *perstictus*, *septentrionalis*. Group of *steinheili*, Australia, New Caledonia, New Guinea: *asper*, *caledonicus*, *cedaris*, *crinitus*, *duchaussoyi*, *occidentalis*, *steinheili*.

### Preliminary Key to Indo-Australian *Sphinctomyrmex* (Workers)

- Antennae 12-merous ..... 2  
 Antennae 11-merous ..... 13
- Large, black or piceous species (WL > 2.0 mm); compound eye of ♀ > 0.20 mm in greatest diameter; pygidial area deeply notched as seen from above (fig. 99; EC & NE Queensland) ..... *turneri*  
 Yellow to black species, smaller in size (WL < 2.0 mm); eyes absent or present as dots in ♀; absent, present as dots, or present and small but multifaceted, in ergatoid queen; pygidium as seen from above truncate in ♀, concave in ergatoid queen ..... 3
- Dorsum of trunk and node and posterior half of sides of head with at least some smooth, shining intervals between foveolae, though such intervals may be narrow and difficult to see ..... 4  
 Dorsum of trunk and node and posterior half of sides of head finely and very densely foveolate, foveolar intervals lacking or very narrow, punctulate, and opaque; color dark brown, gaster castaneous (New Caledonia) ..... *caledonicus*
- Foveolar interspaces on sides of head, dorsum of trunk, and petiolar node very narrow, even in the middle, so that these surfaces appear opaque except in exactly the right light and viewing angle ..... 5  
 Foveolar interspaces on sides of head, dorsum of trunk, and petiolar node often broad, smooth or alutaceous, strongly shining, especially near midline ..... 6
- Larger species, TL 4.8 mm (NW Australia) ..... *perstictus*  
 Smaller species, worker and ergatoid queen TL < 4.5 mm (N Queensland) ..... *asper* [73]  
 Sides of head as seen in full-face view almost perfectly straight, even very feebly concave near midlength, posterior corners very sharply rounded, almost rectangular; punctures of head very coarse, many contiguous or subcontiguous (Australia: Darwin dist.) ..... *septentrionalis*

- Sides of head as seen in full-face view slightly to strongly convex throughout, posterior corners obtusely rounded; punctures of head varying with species ..... 7
7. Color "black" (according to Clark); head "finely and densely punctate" (NE New South Wales) ..... *nigricans*  
Color yellow to dark, reddish brown ..... 8
8. Dorsum and sides of head covered with numerous fine and coarse punctures, with these mostly separated by smooth, shining interspaces; color yellow to medium ferruginous in full adults ..... 9
- Dorsum and sides of head covered with coarse punctures and umbilicate foveolae, mostly contiguous and subcontiguous; color ferruginous to deep reddish brown in full adults ..... 10
9. Mandibles finely striolate over basal  $\frac{2}{3}$  in addition to the coarse punctures (E New South Wales) ..... *floggatti*  
Mandibles almost entirely smooth and shining between coarse punctures; striolation, if any, limited to a small patch near inner margins (SE & SW Australia) ..... *umbelici*
10. Foveolae of sides of head mostly arranged in longitudinally contiguous rows with longitudinal costulae between, so that these areas appear coarsely striate-punctate at lower magnifications (SE Queensland) ..... *njobergi*  
Foveolae of sides of head not arranged in contiguous chains with costulae between ..... 11
11. Compound eyes present and multifaceted; species possibly based on an ergatoid ♀ (C coastal Queensland) ..... *myops*  
Compound eyes present only as vague, pigmented dots in worker, without distinct separation into facets ..... 12
12. Larger, light reddish species, TL > 5.3 mm; reclinate pubescence sparse on postpetiole and gaster (Australia: N Territory, Adelaide R.) ..... *clarus*  
Smaller, dark brownish red species, TL usually < 5.3 mm; appressed and decumbent pilosity dense on postpetiole and gaster (figs. 101–102, 105–113; N Queensland) ..... *trux* [72]
13. Pygidium deeply excised as seen from above (fig. 100; India; Burma) ..... 14  
Pygidium rounded or truncate as seen from above (Australia; New Guinea) ..... 15
14. Size larger, WL > 1.4 mm; color deep brownish red; petiolar node longer than wide (fig. 100; Burma, S India) ..... *furcatus*  
Size smaller, WL < 1.4 mm; color light brownish red; petiolar node wider than long (India) ..... *taylori*
15. Smaller species, WL of ♀ < 0.80 mm; of ♀ < 0.90 mm ..... 16  
Larger species, WL of ♀ > 0.80 mm; of ♀ > 1.00 mm ..... 18
16. Punctures of gaster fine (E Australia) ..... 17  
Punctures of gaster coarse (New Guinea) ..... *eribratus*
17. Ergatoid ♀ compound eyes with > 18 facets each (E New South Wales, SE Queensland) ..... *duchaussoyi*  
Ergatoid ♀ compound eyes with < 15 facets each (NE Queensland) ..... *cedaris*
18. Foveolae of dorsum of head nearly all contiguous and with few or no shining interspaces except for the upper middle of the vertex where the ocelli would occur in a ♀; queen ergatoid, with workerlike trunk but compound eyes developed and multifaceted (widespread in forests of E and SE

Australia) ..... *steinheili*  
Foveolae of dorsum of head crowded, but many are separated by narrow, shining interspaces in addition to the spaces in the upper-middle vertex; queen winged or dealate, with developed pterothorax (SW Australia) ..... *occidentalis*

## *Leptanilloides* (transferred from Leptanillinae)

= *Leptanilloides* Mann, 1923:13–15, fig. 1, ♀. Type: *Leptanilloides biconstricta* Mann, by original designation, monobasic.

= *Leptanilloides*: Borgmeier, 1955:652 (loc. cit. infra).

In his monograph of the New World army ants, Borgmeier (1955:652–655, pl. 33, fig. 1a–f) redescribed and figured a worker from the type series of *Leptanilloides biconstricta*, saying of the genus, "So long as the sexual forms and the larvae remain unknown, nothing can be said about the systematic position of this interesting genus. It is safe to say that it cannot be placed with the Ecitonini ..." He thought it was more like *Leptanilla* and *Leptomesites* (subfamily Leptanillinae) but noted that it differed from these in the fused frontal carinae, the carinate cheeks, the short teeth on the anterior border of the head, and the doubly constricted gaster, which "recalls certain cerapachyines (for example, *Sphinctomyrmex*)."

Borgmeier concluded that *Leptanilloides* "shows a mixture of characters of the Ecitonini and Leptanillinae, but cannot be placed easily in either of these groups. Perhaps the concept of the subfamily Leptanillinae should be expanded and a tribe established just for *Leptanilloides*."

A reexamination of the few available specimens left in the MCZ confirms for me what Borgmeier's figures show reasonably clearly: *Leptanilloides* is a cerapachyine close to *Sphinctomyrmex*. In fact, the structures of the front of the head: reduced frontal carinae, approximated antennal insertions, lateral cheek carinae produced angularly beyond the clypeal border, eyes lacking or extremely reduced—all are shared by the two genera. Shared too is the segmentally constricted gaster, with the postpetiole and 3 succeeding segments subequal and separated. In *Leptanilloides*, however, the seventh tergal segment (pygidium) is greatly reduced, ventrally displaced, and covered dorsally by the sixth tergum. But the most obvious, distinctive character of *Leptanilloides* is the strong and apparently flexible (promesonotal?) suture separating the front and rear portions of the trunk, elsewhere found among cerapachyines in the fossil (Baltic Amber) "*Procerapachys*." This is a primitive character that appears to have been lost in most cerapachyine stocks through the rest of the Tertiary. Truncal fusion probably represents an increase in resistance to the bites, sprays, and stings of prey ant species that tried to defend themselves against an increasingly dangerous predator. The southern African *Cerapachys wroughtoni* also has a well-developed promesonotal suture, all the more unusual because this ant is blind, or nearly so, and is almost certainly cryptobiotic in its life-ways.

It would be extremely useful to know the queen, male, and larval forms of *Leptanilloides*, and something of its habits. So far, we know only the workers of the sole species, *L. biconstricta* Mann, 1933:14, from Tumupasa, Bolivia.

## Simopone

- > *Simopone* Forel, 1891:139 ♀. Type: *Simopone grandidieri*, monobasic.
- > *Cerapachys* subgenus *Simopone*: Forel, 1892:243; also *Simopone* subgenus *Cerapachys*, p. 247, lapsus.
- > *Simopone*: Emery, 1911:15-16, pl. 1, fig. 7, ♀ ? ♂, species list.
- > *Simopone*: Arnold, 1915:19-21, diagnosis, 1 S African sp. described.
- > *Simopone*: Santschi, 1923:259-263, 3 C African spp. described.
- > *Simopone*: Taylor, 1963:1-6, review of generic characters, list of spp. —1966:287-290, Indo-Australian spp.

**Worker:** Distinguished from *Cerapachys* in all species by the lack of apical spurs on the tibiae of middle legs. Other *Simopone* characters are the elongate head (2 exceptions) with widely separated frontal carinae forming partial scrobes for the antennal scapes (1 or 2 exceptions), large compound eyes placed at, or in front of, the midlength of the head (1 exception), 11-merous antennae (1 exception with 12 segments), and toothed tarsal claws (sometimes with an extra tooth or lobe at base of claw). Ocelli frequently present or their pits indicated. The petiole is usually more or less depressed and marginate laterally.

Sculpture varying with the species from smooth and shining to finely reticulate or striolate in part, or with spaced punctures. Pilosity usually sparse, the longer hairs tending to be bilaterally positioned.

Color yellow, brown, black or bicolored.

**Queen:** Unknown for most species; in *S. bakeri* a normal dealate form exists, with differences from the conspecific worker paralleling those of *Cerapachys*.

**Male:** The diagnosis given by Emery (1911:15) applies only doubtfully to *Simopone*. In fact, the male caste of this genus has yet to be described from specimens certainly associated with workers or queens.

**Larva:** The larva of *S. conciliatrix* (as "*Simopone* n. sp.") has only recently been described by G. C. and J. Wheeler, 1974:103-104, fig. 2. It is much like the larvae of *Cerapachys* but has small mouthparts, including peculiar multidentate mandibles.

**DISTRIBUTION:** *Simopone* is widespread but sporadic in the wet, Old World tropics, from Natal in South Africa through Central and East Africa and Madagascar, and in the Indo-Australian region from southeastern Asia to New Guinea and the Philippines. The genus is uncommon in collections, probably because of its predominantly arboreal habitat, and the distribution is probably wider than known at present.

**BIONOMICS** discussed under the tribal rubric above.

## SIMOPONE species

- (T) *bakeri* Menozzi 1926:92 ♀ Singapore
- (T) *chapmani* Taylor 1966:287 ♀ Philippines
- (T) *conciliatrix* Brown n. sp. ♀ W Africa [77]
- (T) *conradi* Emery 1899:475 ♀ Cameroon
- (T) *emeryi* Forel 1892a:247 ♀ Madagascar
- (T) *fulvirodis* Santschi 1923:262 ♀ C Africa
- (T) *grandidieri* Forel 1891:141 ♀ Madagascar

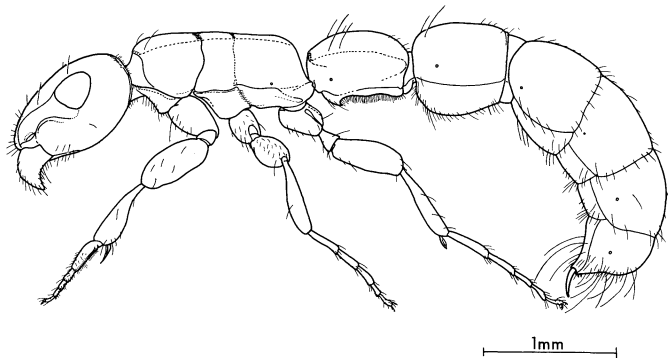


Figure 5. *Simopone gressitti*, side view of holotype (after R. W. Taylor).



- (T) *grandis* Santschi 1923:259 ♀ C Africa [76]  
*gressitti* Taylor 1965:3 ♀ W New Guinea  
*laevissima* Arnold 1954:291 ♀ Uganda  
*marleyi* Arnold 1915:20 ♀ S Africa:Natal  
 (?) *mayri* Emery 1911:116 ♂ Madagascar  
 (T) *schoutedeni* Santschi 1923:260 ♀ C Africa [78]  
 (T) = *usuburi* Weber 1949:7 ♀ n. syn.

## Key to *Simopone* of Continental Africa (Workers)

1. Antennae with 12 segments (small, shining, yellow species with elongate petiolar node, figs. 11, 12, 13; C and W Africa) ..... *concordia* n. sp. [77] 2  
 Antennae with 11 segments ..... 2
2. Large black species, petiole  $W > 0.9$  mm; hind metatarsi each with a deep, elongate groove or opening at the base of the flexor surface, facing the tibial spur (C Africa, figs. 87, 103, 104) ..... *grandis* [76]  
 Smaller forms, petiole  $W < 0.9$  mm; hind metatarsi with at most a fine, impressed line at base of flexor surface ..... 3
3. Posterodorsal border of petiolar node slightly to markedly concave in outline as seen from above ..... 4  
 Posterodorsal border of petiolar node straight to weakly convex in outline as seen from above ..... 6
4. Most of dorsum of head, dorsum of trunk, middle of petiolar disc, and postpetiole finely, longitudinally striolate and subopaque (black, with ferruginous appendages; W Africa) ..... *conradi* [78]  
 Most of the body smooth and shining, with separated punctures ..... 5
5. Black; head only slightly longer than broad (CI  $> 75$ ; Uganda) ..... *laevissima*  
 Yellowish; head narrower (CI  $< 75$ ; Natal) ..... *marleyi*
6. Main part of head and body black; pilosity abundant and generally distributed; petiolar node about as wide in front as behind (C Africa) ..... *schoutedeni* [78]  
 Main part of body piceous to black, except petiole and postpetiole, which are predominantly yellow; longer hairs of pilosity sparse, bilaterally paired on humeri, and in sparse rows on posterior margins of gastric segments; petiolar node distinctly narrowed in front (C Africa) ..... *fulvinodis*

## TRIBE CYLINDROMYRMECINI

The tribe includes the sole genus *Cylindromyrmex*, described and discussed immediately below.

### *Cylindromyrmex*

- > *Cylindromyrmex* Mayr, 1870:967, ♀. Type: *Cylindromyrmex striatus*, monobasic. — 1887:544, ♀ ♂.  
 > *Cylindromyrmex* Emery, 1911:14-15, pl. 1, fig. 6, ♀ ♂ ♂, species list.  
 > *Holoponera* Cameron (not Mayr), 1891:92, ♀. Type: *Holoponera ulmiperi*, monobasic. Syn. Emery, 1901b:54.  
 > *Ceratopachys* subgenus *Cylindromyrmex*: Forel, 1892a:243.  
 > *Cylindromyrmex* subgenus *Cylindromyrmex*: Wheeler, 1924:106, key to spp.  
 > *Cylindromyrmex* subgenus *Hypocylindromyrmex* Wheeler, 1924:106. Type:

*Cylindromyrmex longiceps*, by original designation. Syn. Brown, 1973: 181.

> *Cylindromyrmex* subgenus *Metacylindromyrmex* Wheeler, 1924:106. Type: *Cylindromyrmex godmani*, by original designation. Syn. Brown, 1973: 182.

> *Cylindromyrmex*: Menozzi, 1931:191-195, key to spp., p. 194 — Santschi, 1932:410-412, *Metacylindromyrmex* doubtfully distinct, p. 411. — Wheeler, 1937:441-445, includes key to ♀ ♂ species, p. 444; virtual synonymy of *Metacylindromyrmex*, p. 443.

= *Cylindromyrmex*: Krombein, 1972:91, subgenera *Cylindromyrmex* + *Hypocylindromyrmex*, species lists.

**Worker:** Essentially monomorphic but varying considerably in size, even in uniserial series. Color reddish brown to black or piceous; appendages yellow to black, or dark with the tibiae extensively marked with yellow or ivory. Integument thick and hard.

Head longer than broad, and deep dorsoventrally; sides parallel, with blunt posterior corners and concave posterior border. Clypeus short, crowded by the antennal insertions and the frontal carinae, which approach or reach the anterior margin of the head; in the latter case, the median section of the clypeus is vertical. Posteromedian section of clypeus extending posteriad between the nearly approximate frontal lobes as a deeply sunken groove that broadens very slightly behind to encompass the tiny frontal area, which is not or barely distinguishable. Frontal carinae subparallel behind, where they arise more or less near the cranial midlength, curving mesad anteriorly to form a rounded plate or twin blunt points at or above the main part of the clypeus. The carinal lobes are extended laterad in the form of broad laminae roofing the medial sides of broad antennal scrobes that extend forward from the level of the eyes to the antennal insertions. Behind median groove, space between carinae is broad, flat, or gently convex. Ocelli present or absent. Antennae very short, broad, and flattened, 12-merous; scape only about 2-3 times as long as broad, and not, or just barely, reaching the eye; funiculi gradually broadened toward apices; a vague club formed of the 3 apical segments, or no club distinguishable; apical segment as long as, or longer than, the 2 preceding segments taken together. Mandibles subtriangular, thick and slightly downcurved; apical and basal borders distinct and meeting at an angle; apical border with 4-10 low teeth or crenulations, sometimes virtually edentate, but with a more or less acute apex. Maxillary palpi with 2 segments, labial palpi with 2 or 3 segments; mouthparts of *C. striatus* described by Gotwald 1969:43, 47, pl. 31. Compound eyes situated near or behind cranial midlength, ranging from small and flat, with 20 or less indistinct facets, to large and moderately convex, taking up nearly 1/2 length of the sides of the head and having 500 or more facets.

Trunk elongate, boxlike, with subparallel, vertical sides and a gently convex dorsum (sometimes nearly flat); dorsal sutures represented at most by a feeble, promesonotal, arched line and a weakly indicated metanotal groove with

a median pit, but often these sutures are obliterated. Lateral sutures reduced to an inverted U- or A-shaped system outlining the mesopleuron. Pronotum not transversely marginate in front, humeral angles rounded; propodeal declivity distinct and flat or nearly flat, but not, or bluntly, margined laterally and above. Propodeal spiracle situated below the middle axis of the trunk, round, oval, or elliptical, opening directed dorsad and usually slightly caudad. Metapleural gland opening a horizontal slit very near the bottom edge of the trunk (below a rather prominent bulla); a horizontal groove extends forward along the lower side of the trunk to the vicinity of the mesometanotal suture.

Petiolar node subcuboidal, usually a little longer than high and about as broad as long, a little broader behind than in front, sides slightly convex and vertical (receding ventrad); subpetiolar process stout and bluntly angular in front, subsiding concavely behind. Postpetiole much wider than petiole, wider than long, and almost as wide as succeeding (first gastric) segment, from which it is separated by a wide pretergital belt belonging to the latter; constriction between these two segments is marked, especially in side view. Stridulatory file present and extremely fine on middle of first gastric segment pretergite but not readily visible unless gaster is flexed.

In *C. striatus*, Gotwald (1969:126) found the tergum and sternum of the postpetiole (true abdominal somite III) to be fused, while in the succeeding segment, which I call the "first gastric" in this paper, the tergum and sternum are connected only by membrane, as are those of the segments following. The first gastric segment is larger than the postpetiole and the second and third gastric segments, but not markedly so, and these segments are well developed, mobile, and extend free. Apical (VII true abdominal) somite well developed, tapered caudad, the tergum flattened (obliquely truncate) and margined along the sides with subreclinate spinules that appear to be short, stout setae in raised sockets, arranged on each side in a more or less regular single row. The pygidium itself ends in a pair of blunt, flattened teeth lying just above the sting, which is well developed and tends to be curved in a sword shape (laterally compressed) and usually is extruded part way.

Legs stout, moderate to short in length; femora dorsoventrally incrassate and anteroposteriorly compressed, their flexor surfaces with a long, deep sulcus to receive the curved flexor surface of the tibia when the leg is folded. Tibiae more or less incrassate, especially in the assumed cryptic-foraging small-eyed species; apical spurs long, broadly pectinate, especially on foreleg; middle and hind legs each with an extra, small, pectinate outer spur next to the large one.

Metatarsus, especially that of middle leg, extremely variable in proportions: long and slender in *C. striatus*, much shorter and broadened apically in the small-eyed species, with a semicircle of 4-5 stout, spinelike setae on

the outer apical edge, best developed also in the small-eyed species, where the middle legs may serve (along with the pygidium) as "pushers" in helping the ant through narrow cracks or passages in soil or rotten wood, perhaps through defensive walls being raised by termite prey.

"Pusher legs" are also found in the termite predators of tribe Acanthostichini, in genera *Centromyrmex* and "*Wadeura*" (*Pachycondyla*) of tribe Poncini, in *Cryptopone* (prey unknown) of the same tribe, and in the termitophorous myrmicine genus *Metapone*; in *Melissotarsus*, similar middle legs bear glands that may have a very special use in marking trails along the substrate above the ant's body as it moves along (see Delage-Darchen, 1972, *Insectes Sociaux* 19:213 ff.).

Other tarsal segments also with 2-5 spinelike setae at apices. Claws simple, thickened basally.

**Queen:** Like the worker, and usually only moderately larger. Compound eyes larger, and pterothorax developed, but with a flat dorsum continuing the flat or feebly convex dorsal surface of the trunk.

**Male:** Similar in size to the conspecific worker, but body more slender; head shorter, subglobose, with very large convex eyes taking up more or less the anterior half of the sides of the head. Antennae long and slender, 13-segmented, with very short, cylindrical scape, even shorter, cup-shaped pedicel, and remaining flagellar segments long and subcylindrical.

Frontal lobes short, raised, separated in front, but fused behind. Clypeus with a broad, sloping anterior part and a narrow posterior part between frontal lobes. Mandibles substantial, narrow-subtriangular, with curved, edentate (culturate) apical margins and an acute, incurved apical tooth. Mandibles crossing over each other at full closure, leaving no anteclypeal space. Palpi segmented 2,2 or 2,3.

Trunk compact and subcylindrical, pterothorax only gently convex and slightly raised above truncal outline. Notauli present (*C. parallelus*) but incomplete behind, not meeting as a Y or V. Metanotum small, transversely elliptical. Propodeum long, declivity nearly perpendicular and with a very strong margin and a vertical median septum or carina.

Wings with complete poneric venation, but *Mf*<sub>2</sub> and *r-m* have wide breaks, apparently at the crossings of a fold line; radial cell fairly short, closed apically at or very near the margin. Pterostigma thick, convex, heavily pigmented. Hind wing with distal free abscissae ending near mid-wing; *r-m* weak and broken; anal lobe lacking.

Legs short and only moderately robust; anterior and middle coxae inserted far apart. Middle and hind tibiae each with 2 pectinate apical spurs, one larger than the other. Tarsal claws simple but with thickened, sometimes angular bases.

Petiole much like that of worker; anterior face steep and marginate. Subpetiolar process present. Postpetiole only a little wider than petiole and not much narrower than gastric segments I-IV, which are subequal among themselves

in length and width; postpetiole separated from gaster by a distinct constriction. Pygidium bluntly rounded; hypopygium ending in paired, long posterior spines (fig. 117) and a short median tooth (in *C. parallelus*). Genital capsule complete; parameres tend to be divided into basal and distal pieces (gonocoxites and gonostyli?); the capsule of *C. parallelus* is shown in fig. 130.

Integument coarsely striate as in worker and queen, but the pterothorax (including pleura) are largely smooth and shining, with numerous, fine punctures; postpetiole variably sculptured; striate, longitudinally rugulose, or partly reticulate; gaster shining, very finely reticulate, and with scattered punctures.

Pilosity fine, short, predominantly decumbent. Color black, legs and antennae often prevailing yellow or light brown.

Wheeler (1937:443) already gave justification for synonymizing his own subgenus *Metacylindromyrmex*, based on the 2 spurs on the hind tibiae; but these spurs are present on both middle and hind tibiae in all of the species I have seen. The subgenus *Hypocylindromyrmex* is distinguished by the small, flat eyes of the worker and the longitudinal striation of at least the basal part of the first gastric (IV true abdominal) tergum. It seems to me that this distinction is rather a weak one, deserving recognition at the species-group level at most. Furthermore, Wheeler's own *C. darlingtoni* from Cuba has eyes of intermediate size, and these are slightly convex.

Another new group character needs to be considered: the metatarsus of the middle leg in the *Hypocylindromyrmex* workers and queens is very short and subtriangular, broadened rapidly from base to apex, and bears an apical circlet of 3-4 stout, conical spinelike setae, at least 2 of which are directed laterad. This metatarsus is only about twice as long as its greatest breadth, less than half the length of the whole tarsus of which it is a part, and also less than half the length of the metatarsus of the hind leg, which is itself rather short but still cylindrical. In *C. striatus* and *C. brasiliensis*, the middle metatarsus is slender and elongate, more than 4 times as long as broad, and similar in proportions to the considerably longer metatarsus of the hind leg. *C. darlingtoni*, *C. meinerti*, *C. brevitarsus* and *C. parallelus* all have the short middle metatarsus, but an intermediate condition holds in the queen of *C. boliviae*, for which the worker is still unknown. In this last species, the middle metatarsus is almost 3 times as long as its greatest (apical) breadth. So far as known in this genus, queens and workers are alike in appendage characters and it would be interesting to know if the worker of *boliviae* is intermediate in eye size as well as metatarsal proportions. In any case, known intermediates connect the extreme *Hypocylindromyrmex* to *Cylindromyrmex* for each of the 3 known "diagnostic" characters, and I do not think a formal division can be maintained.

**BIONOMICS:** The species of *Cylindromyrmex* nest in cavities in sound or rotten wood, under bark, in hollow stems of

standing or fallen plants such as the castor bean, and in similar situations. The small-eyed species are evidently more cryptic in habits than are large-eyed forms such as *C. striatus*. The workers and even nests of several species have been found in termite galleries, and males and queens of *C. parallelus* collected in a log on Barro Colorado Island, Panama Canal Zone, by A. E. Emerson, are pinned with workers and sexual forms of a termite in the MCZ. Consequently, the old assumption that the genus is termitophilous is probably correct. Still, it would be useful to have some detailed observations on the feeding habits.

**DISTRIBUTION:** New World tropics, from Central America to southeastern Brasil and Bolivia; Galapagos Islands.

## CYLINDROMYRMEX species

- (T) *boliviae* Wheeler 1924:104 ♀ Bolivia; Venezuela [80]  
 (P) *brasiliensis* Emery 1901b:53 ♀ S Brasil  
 (P) *brevitarsus* Santschi 1924:5 ♀ S Brasil  
 (T) *darlingtoni* Wheeler 1937:441 ♀ Cuba  
*godmani* Forel 1899:4 ♀ Panama; Ecuador  
*longiceps* André 1892:47 ♀ Brasil  
 (T) *meinerti* Forel 1905:155 ♀ Venezuela  
 (P) *parallelus* Santschi 1932:410 ♀ Panama  
*schmidti* Menozzi 1931:191 ♀ Costa Rica  
 (P) *striatus* Mayr 1870:967 ♀ Guyanas; Ecuador; Peru; Galapagos [79]  
 = *whymperi* (Cameron) 1891:91 ♀ (syn. Emery, 1901b:54)  
 (T) = *williamsi* Wheeler 1924:101 ♀ n. syn.  
 = *tibialis* Stütz 1932:367 ♀ n. syn.

I have not attempted to make a full revision of the *Cylindromyrmex* species, though such a revision is probably needed. The material available is insufficient, especially seeing that some crucial specimens are headless or otherwise seriously damaged. A proper revision will require more series with workers and queens associated. I offer instead a modification of Wheeler's key of 1937:444-445. Users should be warned that the measurements as given may be imprecise, especially those derived from Wheeler's own descriptions. Most will be undermeasurements as compared to dimensions cited elsewhere in this part for other genera, and the smaller the absolute dimensions of the insect, the greater the error is likely to be.

## Key to *Cylindromyrmex* Species (Workers and Queens)

1. Workers . . . . .	2
Queens . . . . .	8
2. Eyes small and flat; at least the first gastric (IV true) abdominal segment partly longitudinally striate . . . . .	3
Eyes large and convex; gastric terga smooth . . . . .	6
3. Head nearly twice as long as broad; mandibles edentate; "length 8 mm" (Brasil) . . . . .	<i>longiceps</i>
Head not more than 1½ times as long as broad; mandibles dentate . . . . .	4
4. First gastric tergum striate only at base . . . . .	5

- First gastric tergum entirely, and second at least partly, striate, TL 6-7 mm (Panama) ..... *parallelus*  
(Venezuela) ..... *meineri*
5. Body brownish red, head and gaster dark brown or black; mandibles with about 6 teeth; eyes very small, with about 30 or less indistinct facets; "length 4.5 mm." (SE Brasil) ..... *brevitarsus*  
Body black or very dark brown; mandibles larger, with about 10 teeth or crenulations; eyes larger, with > 50 facets; TL 6-7 mm (Cuba) ..... *darlingtoni*
6. Eyes situated at about middle of sides of head; "length 6-6.5 mm" (Costa Rica) ..... *schmidti*  
Eyes situated distinctly behind middle of sides of head ..... 7
7. Coxae, femora, and tibiae uniform ferruginous yellow, tarsi sometimes slightly darker ferruginous (S Brasil; Paraguay) ..... *brasilensis*  
Legs black or dark brown; extensor surfaces of tibiae pale yellow, or at least partly clouded with dull yellow (Ecuador; Galapagos; Peru; Guyanas) ..... *striatus*
8. Postpetiole and gaster smooth ..... 9  
Postpetiole entirely striate above ..... 10
9. Femora yellow; fore tibiae more than twice as long as broad; wings brownish; TL about 10 mm (Bolivia; Venezuela) ..... *boliviana*  
Femora "reddish black," fore tibiae scarcely twice as long as broad; wings violaceous; "length 12.5 mm" (Panama; Ecuador) ..... *godmani*
10. Petiole and postpetiole striate, but gastric terga smooth ..... *striatus* and *brasilensis*; go to couplet 7  
At least the first gastric (IV true abdominal) segment more or less striate ..... 11
11. Gastric striation limited to base of first tergum (IV true abdominal segment); mandibles with about 10 teeth; "length 7.5-8 mm" (Cuba) ..... *darlingtoni*  
Tergum of first gastric segment (at least) entirely striate ..... 12
12. Mandibles 7-toothed; tergum of second gastric (V true abdominal) segment entirely striate, third segment at least partly striate; wings grayish hyaline with infuscated tips (Panama) ..... *parallelus*  
Mandibles indistinctly dentate; tergum of second gastric segment striate only in the middle, third segment smooth; wings uniformly infuscated; "length 9.5 mm" (Costa Rica) ..... *schmidti*

## TRIBE ACANTHOSTICHINI

Though 2 genera, *Acanthostichus* and *Ctenopyga*, are recognized in this tribe, only the first is known for all castes. In *Ctenopyga*, we know for sure only the queen; males assigned to the genus are doubtfully associated, and no worker has yet been described for it. The assumption is that the *Ctenopyga* worker is much like that of *Acanthostichus*, but how many characters they actually share is a matter for conjecture. In any case, the characterization that follows is based only on worker, queen, and male of *Acantho-*

*stichus* and queen of *Ctenopyga*.

**Worker:** Monomorphic, but often varying considerably in size, even in the same nest. Body compact but somewhat elongate, subcylindrical, TL ranging from 3 mm to about 8 mm; integument thick and hard. Head subrectangular as seen in full-face view, longer than broad, with sides parallel or nearly so and straight or gently convex; posterior border transverse, usually concave, at least slightly in the middle; posterior corners broadly to rather sharply rounded. Cranium convex above and below, rather deep posteroventrally and with the posterior profile broadly rounded as seen from the side, without carinae or sutures posteroventrally or ventrally, except for the median suture; only the extreme dorsal cervical margin of the head is carinate, and a pigmented mark extends forward a little way from this carina in the middle, following an apophysis on the internal surface.

Eyes reduced to minute unpigmented discs or pits (in some large workers, traces of ommatidial facets can still be discerned at high magnification) situated dorsolaterally a little behind the cranial midlength. Ocelli absent, side of head anteroventral to eye with a shallow, longitudinal groove or channel running from near midlength of head to mandibular insertion. The groove runs ventrad around the lateral boss at the end of the clypeus and appears to enter the insertion at a point adjacent to a deep, round fossa in the extreme base of the mandible itself, as though it could conduct some liquid material from the side of the head down to the mandibular fossa. It is not clear from the available specimens whether the groove begins at its posterior end with a pore or merely the insertion of a seta situated at that point. Usually 1-3 more setae are found in the groove farther forward toward the mandible. (A groove also exists along the outer margin of the mandible in its apical half, and this is set with long, downcurved setae, but the basal connections of this groove, if any, are not clear.)

Antennae 12-merous, very short and thick, especially the scapes, which are flattened and shield-like, and only about 2-3 times longer than broad, but suddenly narrowed basad. Funiculi markedly but gradually broadened toward apex, most segments wider than long, but apical segment longer than broad. Scapes never reaching much beyond eyes when laid straight back, inserted very close to anterior margin of head and close together. Clypeus reduced almost to the status of an anterior rim of the head, extending back as a narrow median sliver between the nearly approximate frontal lobes, and anteriorly forming a low median lobe or apron that is deeply emarginate in the middle and extends laterad as a low, anterior rim or process fronting each antennal socket. Frontal lobes short, broad, horizontal or obliquely raised, with convex lateral margins becoming concave behind, where they are pinched before terminating well in front of the cephalic midlength. Posterior clypeal lobe and frontal area forming little more than a wide groove between the frontal lobes.

Mandibles thick and downcurved, essentially triangular, but the masticatory margins strongly curving and continued into narrowed apices, so that the blades may appear broadly subfalcate in oblique end-on view. Masticatory borders edentate and cultrate or with a few spaced denticles.

Under mouthparts (described and figured by Gotwald, 1969:43-44) with labrum not much broader than long, shallowly bilobate; galea elongate; palpi segmented 2,3.

Trunk boxlike and solidly fused into a single structure; dorsum flat or only gently convex, joining the vertical or even slightly concave sides at rectangular margins, or narrowly rounding into the sides. Pronotum with rounded or bluntly subangular humeri as seen from above. Dorsal sutures obliterated, except for metanotal groove, which sometimes shows as a slightly impressed line; in this area there is a coarse median pit. Laterally, the promesonotal and mesometanotal sutures are strongly impressed and lead up to their respective spiracles; the metanotal spiracle is lateral, well below the dorsolateral margin. In dorsal view, sides of trunk subparallel, usually a little wider across pronotum, and sometimes feebly constricted near metanotal groove. Propodeum with steep, distinct declivity, margined or submargined on sides, and passing into dorsum through a right angle or sharp curve. Propodeal spiracle round, situated near mid-height of trunk and well in front of declivity margin. Metapleural gland bulla and meatus well-developed.

Legs short and stout, with thick coxae, incrassate to very strongly incrassate femora, and short, apically thickened tibiae. Middle and hind tibiae each with a single, broadly pectinate apical spur; a stout seta usually present on these tibiae may represent a vestigial lateral spur; the middle tibiae also have hairy, roughened, extensor surfaces with short, oblique, setal bristles, as in *Centromyrmex*, *Cryptopone*, etc. Metatarsi of middle legs short, each with a stout, conical, submedian setal spine on outer surface and a circlet of such spines at apex; II to VI tarsal segments also with 2 or more such spines, and some also on tarsomeres of hind legs. Tarsal claws slender, simple.

Petiole boxlike, from above, subquadratic or oblong; from side view, longer than high, sessile, with steep anterior face rounding into flat or weakly convex dorsal face; sides vertical, meeting dorsal face at dorsolateral margins or else rounding sharply into dorsal face; sides parallel or nearly so, straight to weakly convex; node posteriorly broadly attached to postpetiole. Subpetiolar process present, laterally compressed, usually irregularly rounded to angular in side view.

Postpetiole wider, and much deeper in side view, than petiole, about as deep as main gastric segments, or nearly so, rounded in front and with broadly rounded ventral surface; distinctly but shallowly constricted from remainder of gaster. Gaster fairly long, tapered toward both ends, and wider than postpetiole; apical segment downturned, its tergum apically flattened and forming a triangular pygidial

area bordered with short, stout, setal spines; sting well developed.

In general, body smooth, shining, and without coarse sculpture; but in some of the species, wide areas, especially sides and posterior of trunk and dorsal face of petiole, are finely and superficially reticulate or reticulate-striolate, and these areas are opaque or subopaque.

Pilosity sparse, consisting mainly of longish, fine setae that are bilaterally matching on head, alitrunk, and petiole, and a little more abundant on gaster, especially near apex. The antennae, mandibular apices, and legs have some erect or oblique hairs, and the legs also may have very sparse, short, appressed pubescence.

Color varying from yellowish through reddish to dark brown, sometimes in life appearing black to the naked eye.

**Queen:** Like the worker of *Acanthostichus*, but occurs in 2 types, the subdichthadiiform (*Acanthostichus*) and the "normal" (*Ctenopyga*). In the subdichthadiiform type, the body is much larger and broader than in the corresponding worker (body L 10.5 mm in *A. quadratus*, according to Emery, and 12 mm in the *A. laticornis* queen, *teste* Bruch), the head is almost circular in full-face view, and the flat compound eyes, while still small (not longer than the width of the median funicular segments), are distinctly multifaceted. Ocelli lacking or represented by small pits. Frontal carinae deflected strongly behind, laterad toward the eyes, forming demisircles for the antennal scapes. Mandibles short but subfalcate, edentate, but each with an acute apex, blades narrower than in worker. Antennae and palpi much as in worker, perhaps a bit more slender. Trunk workerlike in form but much wider, and as wide behind as in front or slightly wider. Node of petiole much wider than long, with rounded sides; broader behind, and very broadly attached to post-petiole segment. Postpetiole nearly as wide as succeeding (IV true abdominal) segment and not separated from it by a distinct constriction — at least not in dorsal view — so that it forms an integral part of the gaster. Pygidium not bordered with spiniform setae. Gaster including postpetiole quite voluminous and taking up more than half the total length of the body.

Sculpture mostly smooth or sparsely punctulate on head, trunk, and petiole; sides of trunk finely reticulate or reticulo-striolate; pronotum smooth or punctulopubescent. Gaster, at least true abdominal terga IV-VII, densely punctulopubescent and subsericeous. Head, trunk, legs, and petiole with or without long, fine, erect hairs, and the gastric apex with erect pilosity.

Figures of the dichthadiiform queen are given by Emery 1895 and 1911, and by Bruch 1934.

The "normal" queen (*Ctenopyga*) is the kind of winged or dealate female that one would expect to go with the workers of *Acanthostichus*; this queen has fairly large compound eyes, ocelli, and a well-developed but low pterothorax that bears, in the virgin state, apparently functional wings. I have not studied such a queen directly, but the

good figure in M. R. Smith (1947:526, pl. 1, fig. 4, 529) shows an insect very much like the *Acanthostichus* workers we know from South America. The cheek grooves, a worker character described here for the first time, have not been checked for on the extant *Ctenopyga* (or *Acanthostichus*) queens. Wing venation unknown.

**Male:** (*Acanthostichus*): Body size similar to, or slightly greater than, the corresponding workers, but appearance quite different. Head broader than long, including the large compound eyes, which occupy nearly half to more than half of the head length. Ocelli well developed.

Antennae 12-merous, with short scapes, often with incrassate funiculus, tapered distad in apical segment. First postpedicellar (second funicular) segment very small. Frontal carinae short, with lobes raised more than in worker, forming a more or less boat-shaped median frontal area. Clypeus narrow, with a narrow posterior lobe between frontal lobes; anterior part steeply sloping forward, with a more or less distinct, free lamelliform margin.

Mandibles triangular, with tapered apices and edentate, hollow-curved masticatory borders, tips crossing at full closure. Under mouthparts much as in worker; palpi segmented 2,3. Pronotum narrower than pterothorax, the latter not strongly humped. Trunk robust, with well developed wings (fig. 73) having complete or nearly complete venation; in some species, Rs<sub>2</sub>+3 is absent. No anal lobes on hind wings. Notauli absent or at most weakly indicated at the anterior end, incomplete behind.

Legs fairly long and slender, without the stout spiniform setae of the worker; tibial apices each with a single, narrow pectinate spur; claws slender, simple.

Petiolar node somewhat like that of worker but longer, more slender, subpedunculate in front; the node with sloping anterior face, broadest near front or midlength, slightly constricted posteriorly, but broadly attached to postpetiole; subpetiolar process absent or poorly developed. Postpetiole narrow in front, with a sharp transverse ventral lip; broadened caudad.

Gaster fairly long, subcylindrical, often with a pair of light, unpigmented spots beneath on the first segment near the anterior sternal corners; distinct constriction between postpetiole and first segment. Pygidium rounded, with rounded cultrate apical border; cerci vestigial, membranous, not normally exposed in dried or alcoholic specimens. Genital capsule with all main primitive formicid parts; parameres not divided into basal and apical (gonostyli) pieces; aedeagal plates coarsely serrate on ventral edges and with a beaklike, differentiated apex (figs. 140, 141). Parameres rather short; laciniae longer, usually with thickened apices bent outward, overlapping ends of parameres when the capsule is partly extended. Subgenital plate ending in a pair of long, acute, subparallel or diverging spines, usually somewhat upcurved apically.

Sculpture mostly more or less shining, smooth, but the head often minutely roughened and with scattered coarse or fine punctures; coarse punctures (often elongate or even

sulciform) on truncal dorsum, or trunk longitudinally striate dorsally and on sides. Mandibles usually rugulose and hairy. Petiole, postpetiole, and gaster densely punctulate, moderately shining. Body covered with abundant short, brownish, oblique pilosity. Color castaneous to dark brown, nearly black.

**DISTRIBUTION:** Two genera, *Acanthostichus* and *Ctenopyga*, confined to the New World: southwestern United States to northern Argentina.

## *Acanthostichus*

> *Acanthostichus* Mayr, 1887:549 ♀ ♂. Type: *Acanthostichus serratulus* (= *Typhlopone serratulus* F. Smith), monobasic.

> *Acanthostichus*: Emery, 1895a:748-752; pl. 14, fig. 5a-d; pl. 16, fig. 5, 6; pl. 17, fig. 12, 13; ♀ ♂ ♂; 3 n. spp. described.—Emery, 1899: 4, pl. 2, fig. 5a-d, larva.—G. C. Wheeler, 1950:109, fig. 2, larva.

> *Acanthostichus* subgenus *Acanthostichus*: Emery, 1911:13, pl. 1, fig. 4, 4b, 5, ♀ ♂ ♂ diagnoses, species list.

> *Acanthostichus*: Bruch, 1925:110-114, pl., ♀ ♂ larva, pupa.—Bruch, 1934, ♀ ♂ ♂.

= *Acanthostichus* (s. str.): Kusnezov, 1962, synopsis.—Kempf, 1964b, critique of Kusnezov synopsis.

= *Acanthostichus*: Kempf, 1972:10, species list.

≈ *Typhlopone*: F. Smith, 1858:111, ♀.

The worker, queen, and male are characterized above under the tribe.

**BIONOMICS:** The species of *Acanthostichus*, so far as known, are termite hunters. In keeping with the dichthadiiform queen known for some species, the behavior and raiding organization is very army-ant-like in at least some of the tropical forms. Karol Lenko and I found a column at midday raiding a termite nest in the floor of the forest near Benjamin Constant in Brazilian Amazonas. These were robust, dark brown ants of an undetermined species. The column moved mostly beneath the leaf litter and had made a substantial cache of dead worker termites beneath a piece of bark lying on the ground. From the cache, a column led to a crevice in the ground under the roots of a tree, and we could not reach the nest. We saw more than 50 workers, which were probably only a small part of the column. The workers move rapidly and remind one of army ants by the way they walk and use their antennae.

**DISTRIBUTION:** South America east of the Andes and south into northern Argentina; one doubtful species, *skuarrae*, in southern Mexico.

**SPECIES-LEVEL TAXONOMY:** Kusnezov (1962) gave a review of *Acanthostichus* with rather full notes on the biology of some species, a discussion of the taxonomy of certain forms, and a key to the species modified from an earlier one by Wheeler (1934:162). Kusnezov's paper was published in Spanish in a journal not readily available to many potential users, but even so, I have not attempted to translate or revise the key here. In the first place, a later paper by Kempf (1964) criticized the Kusnezov review for accepting too readily the Wheeler key and the taxonomy on which it was based. Kempf also pointed out that some

of Kusnezov's locality records were based on misdeterminations, and that a variety was doubtfully synonymized. Kempf himself did not attempt a revision of the genus because, as he, Kusnezov, Creighton, and others have all declared, the systematics of this group can only be clarified by the study of new material and the critical re-examination of the types of F. Smith, Emery, and Forel. In his *Catálogo*, Kempf (1972) listed the species of *Acanthostichus* s. str., excluding *Ctenopyga* because it came from outside the neotropical area proper.

I find that there is little I can do at this time to further the revision of *Acanthostichus*. Both Kempf and I have obtained a little more material during recent years, and I have been able to examine the types of *A. serratulus* and *A. kirbyi* and to compare them with other material, so that digms are available to the next reviser. But the considerable variation in color, sculpture, and size in the worker samples in collections is great enough to demand that still more material be gathered. The clarification of the species-level taxonomy probably will depend on the association of all the worker forms with their males, since the male genitalia seem to have good characters.

The one important revisionary move I feel should be made now is the separation of *Ctenopyga* from *Acanthostichus*. This is explained below under the *Ctenopyga* generic heading.

#### ACANTHOSTICHUS species

- (T) *brevicornis* Emery 1894a:142 ♀ Guyanas; Brasil; Argentina = *ramosmexiae* Bruch, 1924:260 (syn. Kusnezov, 1962)  
 (T) *femorialis* Kusnezov 1962:126 ♀ NW Argentina; SW Brasil  
*fuscipennis* Emery 1895a:752 ♂ Brasil; Pará  
 (T) *kirbyi* Emery 1895a:751 ♀ Paraguay; SW Brasil; N Argentina  
*laticornis* Forel 1908:345 ♀ Paraguay; Uruguay; N Argentina  
 = *obscuridens* Santschi 1934:23 ♀ (syn. Kusnezov, 1962:131)  
 (?) *niger* Santschi 1933:105 ♀ N Argentina  
*obscuridens* Santschi = *laticornis*  
*quadratus* Emery 1895a:750 ♂ Bolivia; ?Brasil; ?Peru  
*ramosmexiae* Bruch = *brevicornis*  
 (T) *serratulus* (F. Smith) 1858:111 ♀ Brasil; N Argentina  
 (T) *skwarrae* Wheeler 1934:161 ♀ Mexico: Veracruz  
*texanus* Forel 1904:168 ♀, Texas, N Mexico, to *Ctenopyga*  
 (T) = *townsendi* (Ashmead) 1906:29-30 ♀ ♂

#### Ctenopyga

(provisionally restored to generic status)

- = *Ctenopyga* Ashmead, 1906:29-30, dealeate ♀ and ♂. Type: *Ctenopyga townsendi* Ashmead = *Acanthostichus texanus* Forel, by original designation, monobasic.  
 < *Acanthostichus*: Forel, 1904:168, dealeate ♀. —Brown, 1973:179.  
 = *Acanthostichus* subgenus *Ctenopyga*: Emery, 1911:13. —M.R. Smith, 1947, Amer. Midl. Natur. 37:526, pl. 1, fig. 4, 529, ♀. —M.R. Smith, 1955:49-50, synonymy and distribution summarized.

I considered this genus to be a straight synonym of *Acanthostichus* until a very late stage of the preparation of this part of the Reclassification — so late, in fact, that for very compelling reasons, publication can no longer be delayed while I make the studies of type specimens neces-

sary to fully define *Ctenopyga*. Under the circumstances, it might seem better for me to have left things as they stand, with *Ctenopyga*, as considered by most workers, either a subgenus or a synonym of *Acanthostichus*. Such a solution, after all, would only recall the situation in *Sphinctomyrmex*, in which subdichthadiiform queens and winged queens are found in different species of the same genus. In *Acanthostichus*, however, we do not know of any intermediate kinds of queens such as we have in *Sphinctomyrmex*; the queens known for 2 of the 6-8 valid South American *Acanthostichus* species are both subdichthadiiform, while that of the single valid *Ctenopyga* species is large-eyed and winged. The geographical distribution of these forms may also be significant; *Acanthostichus* is South American, with no known representation west of the Andes, in northern Venezuela, or in Central America. Only 1 species, *A. skwarrae*, is known from outside continental South America, and this somewhat aberrant form, from Veracruz, is represented by a single (now headless) worker; it could well belong to *Ctenopyga*, and it must at least be considered as doubtfully belonging to *Acanthostichus*. For what the negative evidence may be worth, no winged or dealeate female "*Acanthostichus*" have yet been reported from South or Central America, at light or otherwise.

Evidence from the males is also noteworthy. The *Acanthostichus* s. str. males so far reported, all from South America, have distinctive 12-merous antennae with the funiculus gradually but distinctly broadened from base toward apex; the pedicel is short, and the following segment (funiculus II) is even shorter. The genitalia of these males (at least 3 species examined, none associated with workers or queens) varies among species, but all specimens have a distinctive aedeagus (figs. 140, 141) in which the valves are broad, each coarsely serrate on the convex ventral margin, with the apex differentiated as a last and largest, beaklike, downcurved point, separated from the serrations by a curved emargination. Such males have been taken on numerous occasions at light at widely separated points in South America, but they are unreported from Central or North America.

The 2 males originally described as *Ctenopyga townsendi* were collected at La Puerta, presumably in Chihuahua, by C.H.T. Townsend. They came on separate pins, and the dealeate queen described with them, from the same locality, was on another pin. So far as I am aware, no males and queens of this species under any name have ever been taken in the nest, in copulo, or in any circumstances that would make it reasonably certain that they belonged to the same species. Apart from locality data, all we have to go on are Ashmead's original assumption that male and queen were conspecific and certain habitus indications that both sexes are "cerapachyine." With these considerations in mind, I belatedly dissected the terminalia of a syntype male of *C. townsendi*, which M. R. Smith (1947, loc. cit. *supra*) has shown to be a junior synonym of *C. texanus*.

To begin with, the *C. townsendi* male has a furciform subgenital plate, but the 2 teeth are much broader and more triangular than in the South American *Acanthostichus*. The parameres and laciniae are also quite different, but these parts can differ considerably between species in *Acanthostichus*. In the valves of the aedeagus comes the big difference; the *townsendi* male type has slender aedeagal valves broadened into thick, angularly capitate apices; the stem-like basal parts are smooth, without any sign of serration along their concave ventral edges. The other fact about the *C. townsendi* male — a character that seems long to have been lost sight of — is that the antennae have 13 segments, with the funiculus not so distinctly incrassate as in most South American *Acanthostichus*. In genitalic and other characters, in fact, the *C. townsendi* type looks more like the numerous light-caught males attributed to *Cerapachys augustae* by M. R. Smith (1942) and others than like the South American *Acanthostichus*. Thus it seems to me that we should face up to the possibility that the assumed male of *Ctenophya texana* (= *townsendi*) is instead the male of some *Cerapachys* species. If the assumed male does in fact prove to be the real male of *C. texana*, then the differences between *Acanthostichus* and *Ctenophya* are widened, and generic distinction is made surer than when it is based upon the queen alone.

Much depends on determining what kind of male and queen go with *A. skuarrae*, and what kind of worker goes with male and queen *C. texanus*. Smith (1955:48-49) mentions an Arizona worker specimen that he did not feel confident in associating with *texanus*. This problem may be solved by other material already in collections, since samples from Sonoran North America have been accumulating rapidly in recent years, but if such samples exist, I have not seen them.

Meanwhile, taxonomic logic seems best served by considering *Ctenophya*, with the sole known species *texanus*, to be a genus apart from *Acanthostichus*. The species *skuarrae* could well belong to *Ctenophya*, but in the lack of hard evidence, it remains formally in *Acanthostichus*. Thus, *Ctenophya* is left with the single species *texanus* (= *townsendi*), for which M. R. Smith (1955) is the appropriate summary reference. *Ctenophya* seems to be centered in the Sonoran zone of Mexico, with extensions into southern Texas, New Mexico, Arizona, and eventually, perhaps, southern California. The best assumption is that, like *Acanthostichus*, it feeds on termites, but this remains to be checked.

## TRIBE AENICOTIGINI

This tribe contains the single genus *Aenicotigon*, which from the beginning was, and still is, known only from the male caste. This genus, recorded only from central Africa, is one of the few really enigmatic ant taxa. Its workers, if they have been described under another generic name, have not been associated with the males, and it seems like-

ly that they are deeply subterranean or otherwise cryptobiotic in habits, and remain undiscovered. All of the males in collections appear to have been taken at light in or near forested areas from Gabon to Zambia, and particularly in Zaire and northern Angola. While not common in arranged collections, one gets the impression that they are not very rare, either, and it seems likely that many specimens exist in unsorted or unstudied collections made at light in the central African area.

So far as I am aware, a plausible queen, winged or otherwise, is still not known for *Aenicotigon*. The most likely reason for this lack is that the queen is a wingless ergatoid or dichthadiiform, or at least a form unable to fly to light. Status as a dichthadiiform would be in keeping with its sometime placement in or near the Dorylinae *sensu lato* and the implications of the name *Aenicotigon*, all of which derive from the somewhat army-ant-like habitus of the male, described under the generic heading that follows.

Forel and Santschi have described 6 species of *Aenicotigon* in addition to the type species, *A. fossiceps*, and these and still other species may be recognizable among the available samples. But a taxonomy of the genus cannot really begin without some knowledge of its workers (if they exist) and queen, and I have felt it advisable to mark time rather than attempt to revise the available male-based species. This means that the taxonomy of *Aenicotigon* is essentially where Santschi (1924, *loc. cit. infra*) left it. All I can do here is to list the species so far described and figure the genitalia of 1 species (figs. 84, 85, 139) as a reminder that male terminalia characters may well be worthy of comparative study.

## *Aenicotigon*

- > *Aenicotigon* Emery, 1901, Bull. Soc. Entomol. Ital. 33:49-51, fig. 3, 4, ♂. Type: *Aenicotigon fossiceps* Emery, monobasic.
- > *Aenicotigon*: Emery, 1910, Dorylinae, Gen. Insectorum 102:27-28, pl. fig. 5, 5b, male. — Forel, 1913f:314-315, 2 n. spp. described from ♂♂. — Santschi, 1924, Rev. Zool. Afr. 12:198-200, fig. 2; 1 n. sp. described from ♂♂, taxonomic notes and key to spp. based on ♂♂.
- > *Aenicotigon* Santschi, 1919, Rev. Zool. Afr. 6:246-248, fig. 2a, b, c; 2 n. spp. and 1 n. var. described from ♂♂ (variant spelling).

**Male:** Long (TL 5-9 mm), slender insect with hypognathous head and long, subcylindrical, downcurved gaster; prevalently smooth and shining, with some punctate areas; color basically tawny yellow (testaceous to yellow ferruginous).

Head somewhat depressed dorsoventrally; as seen full-face oblong, longer than broad without the huge compound eyes, but broader than long if the eyes are included; posterior angles sharply rounded, posterior margin concave, and sides straight or weakly convex, parallel or weakly converging or diverging posteriorly. Compound eyes very large and bulging, their anterior margins reaching the mandibular insertions, occupying half or more of the sides



of the head; inner margins convex; surfaces beset with short, fine, erect hairs. Front of head between eyes deeply concave; clypeus indistinguishably fused with cranium; antennal sockets close together, contiguous to anterior margin of head, which is essentially straight (more or less feebly sinuate), or concave and transverse. Frontal carinae completely fused and reduced to an inconspicuous carina that extends posteriad only a short distance between the antennal sockets before disappearing. Ocelli very large and prominent, set in partial sockets; immediately behind them is a *deep and wide pit* that is peculiar to *Aeniclogiton*. Mandibles wide falciform, inserted far apart, tapering and curving evenly inward to acute apices that overlap at full closure, leaving a wide space between the more basal parts of the shafts; inner margins toothless and cultrate. Antennae 13-merous, rather small and weak for insects of this size; scapes short, incrasate towards their apical halves, about equal to the combined first 5 funicular segments in length, but not reaching much beyond the midlength of the compound eyes when laid back. All funicular segments longer than broad except possibly IV-VII, one or more of which may be as broad as, or slightly broader than, long; pedicel clavate, nearly as long as the next 2 (II and III) funicular segments combined; funiculus distinctly incrasate in its apical 2/3; apical segment longest, but somewhat compressed in dry specimens.

Trunk elongate (2.3-2.6 times longer than wide), especially the pronotum and scutum; the latter takes up much more than half the truncal length. Notauli lacking; long, fine parapsidal furrows present but inconspicuous; in dried specimens, the scutum is usually partly buckled, so that an elongate concave area appears on either side of the dorsal midline. Scutellum simple, convex; metanotum forming a narrow transverse belt; propodeum rounded in both directions (fig. 138). Sides of pronotum and lower posterior half of trunk with broad and fairly deep hollows or sulci, which may be partly due to collapse of the thin integument. Since these hollows are present and similar in 8 specimens belonging to at least 2 species, I assume that they are spaces to accommodate the upfolded legs when the insect is being carried by workers or is feigning death. The pleura are unbroken by long sutures of any kind, except for the complete and strongly oblique one between the pronotum and sides of the mesothorax. Propodeal spiracle small and inconspicuous, situated below mid-height of the trunk; metapleural gland bulla and meatus apparently absent, or at least not visible from ordinary external views.

Wings long and broad, the forewing about as long as the body (minus the head), or longer, with primitive ponerine venation (fig. 137), except for the following: Rsf2-3 detached at base from Rs+M; rarely Rsf2-3 is curved posteriad and weakly attached to Mf3, but usually its base is floating free as in fig. 137. Mf1, though rather strongly oblique, originates well distad of cu-a. Pterostigma large, thick, and heavily pigmented. In the hindwing the

anal lobe is lacking, and, although Rs and M are both usually present, r-m is completely absent. Hamuli inconspicuous, 8-12 (8 specimens examined). Occasionally stubby adventitious veins are found in the forewing, usually issuing posteriad from longitudinal veins. Crossvein cu-a is sometimes weak or absent in the hind wing.

Legs moderate in length; middle and hind coxae very deeply sulcate dorsally, and sharp genual edges are formed on either side of the cleft. Femora laterally compressed but broadened in the extensor-flexor plane, narrowing basad; their flexor edges with a variably extensive apical groove to receive the folded tibia. Tibiae subclavate, broadest in the distal half, the middle and hind pairs all bearing a narrowly pectinate spur and usually a smaller setiform spur. Tarsal segments slender; claws slender, simple.

Petiole (fig. 138) special in shape, depressed, subtrapezoidal, longer than wide to wider than long according to species, with concave anterior margin and slightly produced anterior corners; broadest behind and with prominent, often subacute posterior corners; dorsal face convex in front, but with a broad, shallow median sulcus crossing the summit from the front and widening behind to produce a deep subtriangular excavation that occupies much of the posterior half of the surface. From side view, the petiole is convex above, highest in the anterior half, with rounded front and rear corners; sides rounded and bulging; subpetiolar process a laterally compressed keel with curved outline, steep in front and tapering caudad.

Postpetiole incorporated with gaster, and not separated from gaster by any constriction. As seen from above, the postpetiole tapers anteriorly and is narrowly rounded in front (the narrowly rounded tergal portion overhangs the sternum in front). Remaining gastric segments (true abdominal somites IV through VII) cylindrical, slightly wider than long, subequal among themselves. Postpetiolar tergum and sternum solidly fused; in succeeding segments, terga and sterna are unfused and readily separable. Pygidium (tergum VIII) rounded but not enlarged, with an apical rim (fig. 139); hypopygium forming a robust, slightly up-curved fork with acute, convex-sided prongs and a short, constricted, stalk-like base (fig. 84). Genital capsule partly retractile, with large, expanded, shell-like parameres (fig. 139), a simulanar, non-serrate aedeagus (figs. 85, 139), and small volsella-lacinia differing in shape with the species.

Pilosity consisting of 3 types of hairs: (1) long, fine, flexuous, golden hairs bunched in tufts or rows on mandibles, clypeal margin, scapes, front half of dorsal surface of head and underside of head, along posterodorsal and posterolateral margins of pronotum, along posterior margin of scutum, on sides of mesothorax, on scutellum, on sides of propodeum and posterior corners of petiole (fig. 138), on underside of petiole and subpetiolar process, on femora, tibiae, and hind coxae, and on apex of gaster and terminalia (fig. 139); (2) short to long, appressed to decumbent, straight or slightly curved, golden hairs investing

gaster like a coarse pubescence; (3) very short, fine, curved, erect to suberect hairs forming a sparse but rather even cover on upper (posterior) part of head, outer margins of mandibles, scutal surface, coxae, propodeal dorsum, petiolar disc, tarsae, and antennal funiculi.

**BIONOMICS:** To my knowledge, the only material of *Aenictogiton* found in collections consists of winged males taken at light. At least some of these samples were taken in or near forest or gallery forest, but I do not know the setting of many of the label localities. The habitus of these males certainly is generally like that of some army ants, though they are somewhat smaller than most army ant males. The tufts and fringes of long, golden hairs suggest the similar arrangements ("trichomes," etc.) in many army ant males and in formicid and other insect inquilines in ant nests, and lead naturally to speculation that these males may be adapted towards gaining entrance to colonies of their own or another host species by attracting and offering the host workers allomones that convert or lull their aggressive behavior toward strangers. The army ant males must gain access to alien conspecific colonies to mate with their queens. But the inquiline males must achieve acceptance into the host species' colony in order to work their parasitic mischief.

To me, *Aenictogiton* males have a habitus much like that of the known army ants of the same caste. It is not beyond belief that they could be parasites, but then one would expect to find winged or dealate queens that corresponded to them, and no such queens have been seen. In fact, the lack of queens in collections suggests that they may be wingless and ergatoid or dichthadiiform, as in army ants. The males of *Aenictogiton* lack metapleural gland openings, as do army ant males of all genera, and also some parasitic ant groups. It was my hypothesis

(Brown, 1968, Amer. Naturalist 102:188ff) that the metapleural glands secrete a nest odor, or at any rate an "alien nest" odor, but Maschwitz, Koob, and Schildknecht (1970, J. Insect Physiol. 16:387 ff.) think instead that the gland puts out a substance aimed primarily at reducing micro-organismal contamination. If this were true, then the absence of the gland in army ant males and some inquiline ants could be accounted for by assuming that in these cases, the workers perform the antiseptic lavage. This question still needs investigation.

**DISTRIBUTION:** All of the types of the described species came from Zaire, formerly Belgian Congo. Now I have seen additional material from northern Angola, Zambia, and even from Gabon (Makokou), as well as more samples from Zaire. It does seem as though the distribution of the genus centers on the Congo Basin, and does not extend very far beyond. A number of the records, however, come from localities at elevations of 1000 to 1500 meters, though many are from lower country.

### *AENICTOGITON* species

(References "op. cit." are given previously under the genus. All descriptions are based on males from Zaire, but see above under *Distribution*.)

- (T) *atenuatus* Santschi, 1919 *op. cit.*, p. 247, fig. 2c.
- (T) *bequaerti* Forel, 1913f:314.
- (T) *elongatus* Santschi, 1919 *op. cit.*, p. 246, fig. 2c.
- (T) *emeryi* Forel, 1913f:315.
- (T) *fossiceps* Emery, 1901 *op. cit.*, p. 49, fig. 3, 4.
- (T) *schoutedeni* Santschi, 1924 *op. cit.*, p. 198, fig. 2.
- (T) *sulcatus* Santschi, 1919 *op. cit.*, p. 247, fig. 2a.

(*A. attenuatus* was described originally as a variety of *A. elongatus*, but later, Santschi, 1924 *op. cit.*, p. 199, raised the variety to species rank.)

## APPENDIX

This appendix is meant chiefly to include observations on the taxonomy, distribution, and biology of particular species and species-groups.

[1] *P. tenuis* is known to me only from the type series, collected in "Kamerun" by Conradt. I have selected as lectotype a "cotype" (syntype) worker in MHN—Geneva and labeled it accordingly; types were not available on loan from the Emery Collection, MCSN—Genoa. Lectotype TL 5.05, HL 1.10, HW 0.90, ML 0.25, WL 1.78, scape L 0.76, greatest eye diameter 0.26, distance between eye and mandibular insertion 0.15, petiolar node L (from above) 0.63, W 0.49 mm.

This species is the African counterpart of *P. parallela*, and it closely resembles medium-large specimens of that species; however, *P. tenuis* has larger eyes situated a bit closer to the front of the head (eye length and antocular

distance are usually subequal in *parallela*). Also, *parallela* of the larger sizes have a distinct basal mandibular groove reaching along the outer mandibular border; this is absent in *tenuis* of the same size (and in small *parallela*). *P. tenuis* has the margin or angle complete across the top of the propodeal declivity, whereas in *P. parallela*, the middle of this margin gives way to a more gradual curve of the propodeal dorsum into its declivity. In *tenuis*, the antennal scapes held straight back fall slightly short of the posterior border when the head is viewed full face, while in *parallela*, they slightly surpass the posterior border. *P. tenuis* may also be viewed as a smaller, more slender version of *P. modesta* with short scapes.

[2] A "cotype" (syntype) worker of *P. modesta* in MHN—Geneva is chosen as lectotype ("Kamerun/1895/L. Conradt") and labeled by me as such: TL 7.5, HL 1.38, HW

1.14, ML 0.31, WL 2.34, scape L 1.07, distance between eye and mandibular insertion 0.21, petiolar node L (from above) 0.88, W 0.72 mm. The lectotype is nearer the small end of the size range of available samples assigned now to this species than to the larger specimens. A worker from 10 miles W of Jinja, Uganda, 1200 m (E. S. Ross and R. E. Leech) has HW 1.64, WL 3.14 mm.

Other samples: Kenya: Gilgil to Laikipia (G. Allen and Brooks). Sudan: Khor Aba, Aloma Plateau (J. G. Myers). Zaire: Thysville (Ross & Leech). 62 miles E of Kibombo, 14 Aug. 1957 (Ross & Leech). Gabon: Makokou, rain forest (I. Lieberburg). Ghana: Tafo (B. Bolton). Ivory Coast: ORSTOM Experiment Station, 17 km W of Abidjan (W. L. Brown).

Judging from the description and geographical considerations, I consider it likely that Arnold's variety *matopoenis* belongs to *modesta* rather than to the related Malagasy species *moqueysyi*, to which he originally assigned it. The type locality of var. *matopoenis* is the Matopo Hills, S of Bulawayo, Rhodesia, and the type specimen is probably in the National Museum at Bulawayo.

[3] *P. moqueysyi*, from Antongil Bay, Madagascar, is similar to *P. modesta* but has the 3 teeth of the posterior petiolar margin accentuated almost to the condition of *P. occidentalis*. A lectotype was chosen, a worker "cotype" (syntype) in MHN-Geneva, and labeled accordingly: TL 7.7, HL 1.45, HW 1.33, ML 0.40, WL 2.42, scape L 1.13, greatest eye diameter 0.26, distance between eye and mandibular insertion 0.15, petiolar node L (from above) 1.06, W 0.73 mm.

A type of *P. moqueysyi* var. *debilior* in the Forel Collection was compared directly with the *P. moqueysyi* lectotype, and *debilior* is just a slightly smaller, more slender variant of the species. The type locality of *debilior* is Tulear, SW Madagascar, and also Mahafaly, Madagascar. This species lacks the basal dorsolateral groove of the mandible.

[4] *A. P. frontalis* (type locality: Kamerun, L. Conradt, 1895) lectotype has been chosen from the original "cotype" (syntype) series in MHN-Geneva: TL 8.4, HL 1.64, HW 1.46, ML 0.50, WL 2.76, scape L 1.20, greatest eye diameter 0.33, distance between eye and mandibular insertion 0.30, petiolar node L (from above) 1.00, W 0.83 mm.

The specimen is opaque in general, but a slight shine is reflected from dorsa of trunk, petiole, and gaster in the right light. A worker and queen, accompanied by a male, from the Lamto Ecological Station in central Ivory Coast (J. Lévieux) are like the *frontalis* lectotype but are a little smaller (♀ HL 1.42, HW 1.26 mm) and have notably larger eyes (♀ greatest diameter 0.39 mm; distance between eye and mandibular insertion 0.21 mm). They are black, with reddish mandibles, antennae, tibiae, and tarsi, and the surface is more definitely shining than in the type. Also, they have the petiolar node with the sides

more divergent behind (node wider at rear) than in the type. These Ivory Coast specimens could represent an undescribed species, but since we know so little about the variation of *frontalis*, it seems best to wait for more material before trying to decide about this form.

[5] Types of *P. schultzei* and *P. cyriluli* ("*grili*" on the label in the Forel Collection; "*cyriluli*" is evidently a misprint) were compared in MHN-Geneva, and they are much alike in size, body form, and sculpture. The *cyriluli* types have slightly thicker antennal scapes; the mandibles are reddish, but the antennae and legs are dark reddish brown or brown, not contrasting red as in most samples of *schultzei*. Also, in the *cyriluli* types, the propodeal and posterior petiolar angles are merely subrectangular and not produced, but one of the 3 *schultzei* types in the same collection approaches them in this respect. A type of *schultzei* var. *bequaerti* in MNH-Geneva is just a robust worker of *schultzei*. In the Santschi Collection (NM-Basel), types of *P. schultzei* and its var. *lata* compare well; the variety has a slightly wider petiolar node than usual. The variety *recta* (type in MRAC-Tervuren) is another minor variant of *P. schultzei*.

The MCZ has samples of *P. schultzei* from: Zaire: Kambove, Katanga, 4000-5000 feet (S. A. Neave). 34 miles N of Pweto, 1050 m (E. S. Ross and R. E. Leech). 27 miles SE of Kiengo, 1150 m (Ross & Leech). Zambia: Mumbwa (H. Dollman). Rhodesia: Nantwich (G. Arnold); Wankie National Park, Kulozi River track and near Sinamatella Camp, both in mopane flats, on the ground (W. L. Brown). South Africa, Kalahari Desert, Kabulabula (G. van Son). The Kambove specimen has brown legs. Occasional specimens have a low swelling in the middle of the posterior margin of the petiolar node, undoubtedly a vestige of a median tooth.

[6] Specimens of *P. occidentalis* collected by D. Leston at Tafo, Ghana (BMNH-London and MCZ) are reddish brown in color, HL 1.40, greatest diameter of eye only 0.14, as compared to a maximum scape width of 0.23 mm. In his description of the worker from Uganda, Arnold (1954:291) said nothing about the eyes, though he described the sculpture in some detail and mentioned the diagnostic, very long, second funicular segment. The excision at the top of the propodeal declivity is deep and subrectangular (almost V-shaped). The type of *occidentalis* is a dealate queen from Sierra Leone (MNHN-Paris); this specimen is ferruginous in color and has the 3 strong petiolar teeth characteristic of this species.

[7] The type of *Platythyrea monodi* in MNHN-Paris compares well with type compared digms of *P. conradi* from the Banco Forest Reserve, near Abidjan, Ivory Coast, but the *monodi* type has a very slightly higher and shorter petiolar node. However, some specimens of *P. conradi* from ex-French Congo (det. Santschi) in Paris also show this

variation, while others resemble the *conradti* type. The male of *P. conradti* is distinctive because of the dark-and-light pattern of the wings. I took this species in the Banco Forest from a nest in the hollow trunk of a small living tree; the entrance was about 1.5 m above ground.

The available workers of *P. crucheti* (Angola: Rio Mbale, Sept. 1928, "MSSA") agree with the types of that species. *P. crucheti* is a smaller version of *P. conradti* (see key, p. 10), and further collections in southern Zaire and Angola are needed to show whether it is merely a geographical variant of *P. conradti*.

[8] The Forel-described subspecies of *Platythyrea lamellosa* (*longinoda*, *rhodesiana*, *suturalis*, and var. *grisea* of the last named) all appear to be slight variants of *lamellosa* based on differences in length and punctuation of the petiolar node, characters now known to be very variable in other species of this genus. Males accompany workers in the *rhodesiana* and *grisea* series, and their genitalia are similar externally; the parameres each have a mesial transparent flange.

*Platythyrea arnoldi* is close to *P. lamellosa*, but differs in the continuous profile of the worker trunk and in having the dorsal surface of the node rising gradually to the posterior border, then dropping suddenly into the posterior face, which it slightly overhangs, whereas in *P. lamellosa*, the convex nodal dorsum rounds into the posterior face, which is inclined more or less cephalad. *P. lamellosa* has the mesonotum slightly but distinctly and rather abruptly impressed below the level of the rest of the truncal dorsum. Santschi and others apparently took Roger's description of the *lamellosa* petiolar node as "hinten ganz kurz abgestutzt" too literally. The type locality of *P. lamellosa* is Cape of Good Hope, and it seems very doubtful whether *P. arnoldi* occurs as far south as the Cape Province.

The description of *P. lamellosa apicalis* reads like *P. arnoldi*, and the synonymy of these two names is indicated; *P. viehmeyeri*, incompletely described, is probably also the same as *P. arnoldi*, but since it and *arnoldi* were described in 1913, the priority of the two names is in question. Since the type (and hence the subjective synonymy) of *P. viehmeyeri* is not at present available to me, I can only indicate the problem, but cannot give it a definite solution. *P. arnoldi* palps 4:3.

[9] Wilson (1958:151) began to assemble the synonymy of *P. parallela* during his study of the Melanesian ponerines, when he sank under it *P. pusilla*, *P. coxalis*, *P. melanocholica*, and *P. melanocholica* var. *arana*, the last two names provisionally. *P. melanocholica* originally was vaguely described by F. Smith in 1865 as a *Pachycondyla*, but Emery (1897:556) surmised that the species was a *Platythyrea*, a placement in which he was followed by all later authors when the type of *P. melanocholica* could not be located. However, the type is extant in the Oxford University Collection, where it was found by Barry Bolton, and I was able to

examine it in London in 1973. It proves to be true *Pachycondyla* in the broad sense (*Ectonomyrmex* of recent authors), and so the species *melanocholica* can be eliminated from consideration under *Platythyrea*. It will be dealt with in Part VI of this series.

Wilson was also able to compare digms of the *parallela* complex that I provided for him in 1955 with types of other related forms in European museums, and I have been able to study these and many others abroad and in MCZ in subsequent years, with the result that the synonymy of *P. parallela* is lengthened to include a surprising number of specific, subspecific, and varietal names.

As might be suspected from the length of the list of synonyms, *P. parallela* is a variable insect. The most conspicuous variation is seen in overall body size, as indicated by the length of the trunk (WL), which ranges from about 1.10 to about 2.50 mm in specimens representing more than 50 nest series assigned to this species that I have been able to examine carefully enough. In discussing individual synonyms below, I have given WL for at least one type specimen wherever I was able to make a suitable measurement. I am unable to split the size continuum into modal classes that seem to represent different species, and small, medium, and large forms are known to occur sympatrically at such relatively well-sampled localities as the Cuernos Mts., near Dumaguete, Negros Oriental, Philippines, and on Ceylon. Within single nest series, however, size variation so far as known is relatively narrow in range.

Other variation, as noted by Wilson, occurs in the shape and size of the propodeal angles; in the length vs. width, dorsal convexity, and shape (of the posterodorsal margin) of the petiolar node; in the opacity of the background fine sculpture; in the number and distinctness of the superimposed coarser punctures; in the color of the legs, and other lesser traits. Some preliminary analysis of the length vs. width of the petiolar node by Wilson (1958:152) showed that the larger specimens tend to have disproportionately wider nodes. A rough check indicates that the additional data from the augmented series now available would probably widen Wilson's already fairly wide regression zone, but that the trend would remain the same. On the other hand, the sculptural variation does not seem to be closely correlated with size.

If more than one species is present in this complex, it will take much more refined analysis based on more and better material to reveal it. For the present, the burden of proof is shifted to the splitters, because I am considering the whole complex to represent a single species. Such a treatment only parallels the conclusions reached for other *Platythyrea* species in this study. My notes on the individual synonyms are repeated here, in the approximate chronological order of publication.

*P. parallela* type WL 2.15 mm.; tibiae dark. Sculpture weak, fairly smooth; larger punctures weak, obsolete on pronotum; tibiae dark. Type loc.: Aru Island.

*P. inconspicua* type: dealate queen, tibiae dark brown, WL 2.45 mm., is near the large end of the size range. On my request, Dr. Max Fischer of the Naturhistorisches Museum in Vienna kindly sent 2 specimens, each placed in the Mayr Collection as "*inconspicua*/G. Mayr Typus." Emery mentions these specimens as the two possessed by Mayr, who identified South American samples sent to him by Emery as *P. inconspicua*. One of Mayr's specimens now bears the tiny locality label, "Ceilan/Sichel," and on a larger label below this, apparently in Mayr's handwriting, "Cayenne/wolnicht/Ceilon." The writing is crude and was obviously done in haste; apparently Mayr decided, at some time after the original description, that the specimen was "wohl nicht" (probably not) from Ceylon, and its superficial similarity to the second "Typus," from Panama ("Pergand") further led him to believe that the locality of the first type should have been Cayenne. From this point, it was an easy step to identify Emery's specimens also as *inconspicua*.

A close examination of the original (and only real) type of *P. inconspicua* shows that it is really an Old World tropical member of the genus, and in fact is a large specimen of *P. parallela*. In the first place, the masticatory borders of the mandibles are clearly denticulate or crenulate (in the American species, the border is toothless and cultrate). In the second place, the palpi are very short, and are segmented 3,2, as in other *P. parallela* examined, large and small. Mayr's Panama specimen, on the other hand, has much longer palpi (extending past the posterior margin of the buccal cavity), and the maxillary palpi are 6-merous, the labials 4-merous, as in other members of the *punctata* group. The Panama specimen is in fact a specimen of *P. pilosula*, and cannot be considered as in any way a type of *P. inconspicua*; it was never mentioned in the original description because it had not even been collected by then.

*P. inconspicua* is therefore removed from the synonymy of *P. punctata*, where Emery had assigned it, and is placed as a new synonym of *parallela*.

*P. pusilla* and *P. coxalis* were described in the same paper at a time when the correct generic placement of *Ponera parallela* F. Smith was still unknown, and by this time, Emery had already considered *P. inconspicua* to be a neotropical species (see above). Wilson (1968:151) examined the holotypes of Emery's two species in 1955 and left type-compared digms in MCZ, one of which also compared with *P. parallela*, and the other with *P. wroughtonii*, its subspecies *victoriae*, and *P. parva*. His synonymy of *pusilla* and *coxalis* under *parallela* (1958) seems to me to be correct. The type locality of *P. pusilla* is Amboina, and for *P. coxalis* is Perak, Malaya.

The types of *P. wroughtonii* and *P. wroughtonii victoriae* were examined in the Forel Collection in Geneva. WL of a *wroughtonii* specimen was 1.36 mm, and *victoriae* is a little larger (MCZ syntype WL 1.40 mm). The differences

cited by Forel to separate these forms are very vague, and I was unable to appreciate them in the type specimens; these both seem to me to be small-sized *parallela*. The type localities for *wroughtonii* are Travancore and Mysore (S peninsular India); for *victoriae*, they are Bangalore (in Mysore), Barrackpore (N of Calcutta), and "Inde septentrionale." Both forms have the tibiae light yellow.

The types of *P. subtilis* and *P. pusilla* were compared directly in the Emery Collection (MCSN—Genoa), and I could find no important differences between them; the *subtilis* type is perhaps a little more heavily punctate on the sides of the propodeum and petiolar node. A syntype specimen of *P. wroughtonii* from "Bangalore" in the Emery Collection compares well with these types also. *P. subtilis* type loc.: Pulau Laut, SE Borneo (Kalimantan).

In the Kodeco Tract west of Batulitjin (SE Kalimantan), inland from Pulau Laut, in 1972, I collected several samples of the *P. parallela* complex, including workers of fairly large size (WL 1.81–1.90 mm) and one very small stray worker, the smallest I have seen (WL 1.11 mm), with a fairly short, heavily punctured node with distinct blunt teeth behind. While on the subject of size, I should also mention a single, very large, worker individual (WL 2.50 mm) taken by C. F. Clagg at 5000–6000 feet elevation on Mt. Apo, Mindanao. It is hard to believe that this relative giant is simply a large specimen of *P. parallela*, but it is almost exactly like that species; its eyes are a bit small (greatest diameter 0.13 mm) for such a large specimen, and its second funicular segment is about 1½ times as long as broad (usually about as broad as long in *parallela*), but in other characters, including 3,2 palpal segmentation, it fits *P. parallela*.

*P. coxalis* var. *tritschleri* is a variety intermediate in size between the types of *P. parallela* and *P. wroughtonii* with the lobules of the posterior border of the petiolar node almost completely obsolete. Type locality Indrapura, Sumatra (MHN—Geneva).

*P. coxalis* var. *javana* is similar to the foregoing in size, but the tendency to form 3 low lobes on the posterior border of the petiole is better expressed. In *javana*, the larger punctures are weak and difficult to see. Type locality is Buitenzorg (now Bogor), Java. Both of the above varieties have reddish brown tibiae (MHN—Geneva).

*P. coxalis* var. *annamita* is a little larger than the foregoing (WL 2.12 mm), but seems to belong to the same species. Sculpture fairly weak; tibiae brown. Type loc.: Region of the Mois, central Cochin China. (MHN—Geneva)

*P. wroughtonii* subsp. *sechellensis* has WL 1.55 mm. It has weak, feebly shining sculpture, with small, widely spaced punctures; tibiae yellow. Type loc.: Praslin, Seychelles Is. (BMNH—London.)

*P. coxalis* var. *cylindrica* is a medium-sized queen (WL 1.67 mm) with larger punctures distinct, but reduced in size on pronotum; tibiae brown. Type loc.: Tandjong

Slamat, E Sumatra. (MNHU—Berlin.)

*P. pusilla* var. *australis* is a small form (not measured) similar to *wroughtonii* types; tibiae with yellowish extensor surfaces. Type loc.: Chappall Range and Tambourine Mt., S Queensland. (MHN—Geneva.)

*Platythyrea parva* is like the *wroughtonii* types, but head a bit broader; tibiae with extensor surfaces lightened and yellowish; WL 1.34 and 1.40 on holotype and paratype measured. Type loc.: Darwin, N Australia. (BMNH—London, MHN—Geneva, and MCZ.)

*P. pusilla* var. *egena*: WL 1.51 mm; tibiae more or less pale. Type loc.: Singapore. (MNHU—Berlin.)

*P. coxalis* var. *philippinensis*: WL 1.75, 1.80 mm; tibiae brown. Type loc.: Los Baños, Laguna Prov., S Luzon (MNHU—Berlin, MCZ). Dr. J. W. Chapman assembled large series of *P. parallela* in the Philippines, although many of the specimens were molded or otherwise damaged during World War II. Most of his samples come from the Cuernos Mts. near Dumaguete, Negros Oriental, 1500 to 4000 feet elevation. These vary somewhat in body size and have the legs brown, reddish brown, or with tibiae somewhat lightened in color. Other Philippine samples are from Luzon: Baguio (Chapman); Los Baños (F. X. Williams); Mt. Makiling (A. L. Cambre); Mindanao: Davao City (A. Reyes), Mungangan (no collector), Miatan, Katipunan (D. Empeso); Romblon, Cabrador I. (L. Morato). Borneo: Kuching, Sarawak, (Hewitt); Sandakan (C. F. Baker); Mt. Dulit, N. Borneo, 3000 ft (E. Mjöberg). Gilolo I.: Kalam (C. S. Banks). S. Celebes: Balampsoang Forest, near Tanete (W. L. Brown).

*P. parallela*: WL 2.00 mm; tibiae pale. Weakly shining in most lights, but some small punctures extend onto pronotum. Petiolar node L 0.63, W 0.60 mm, posterodorsal border of node sinuate as seen from above. Eyes a little smaller than in New Guinea *parallela*. Type loc.: "Walde bei Trial Bay," New South Wales, Australia. (MNHU—Berlin.) Additional material from N.S.W.: Jenolan Caves (J. C. Wiburd), Bulga (W. W. Froggatt), Dorrigo (W. Heron), Royal National Park, 25 m elevation (E. S. Ross and D. Q. Cavnagaro), as well as Brisbane, Queensland (H. Hacker) is much like the *cephalotes* type. Smaller specimens come from the McIlwraith Range, Cape York Peninsula, Queensland (P. J. Darlington).

*P. melancholica* var. *arua* was synonymized with *parallela* by Wilson provisionally because the type was unavailable. The type locality is Wammar in the Aru Archipelago, and Aru is the type locality of *parallela*. Upon reading Karaviev's description again, I can only conclude that Wilson's synonymy is reasonable even in the absence of the *arua* type.

*P. pulchella*: the type in NM—Basel is an alate queen from Medan, Sumatra (Corporaal). Node rather short, only slightly longer than broad, but with a sinuate posterior margin as seen from above. Scares and tibiae whitish, prominent against black of remainder of body.

*P. pusilla* var. *pacificus* was put into the synonymy of *P.*

*parallela* by Wilson and Taylor (1967:20), with good reason in my opinion. Type loc.: Apia, Upolu, Samoa.

*P. ceylonensis*: WL 1.86 mm; tibiae brown. Type loc.: Ceylon. (BMNH—London.) This last synonym in the long list is just a fairly large *parallela* queen and workers. Other specimens from Ceylon are from Yakkala (KLA Perera), and Soans and I took a series of slightly larger body size (WL 1.70–1.74 mm) in Kerala State, S India: Peria Reserve, Cannanore Dist., 4 April 1969, tropical evergreen forest, ca. 900 m. Other samples from the SE Asian mainland are: Thailand: E slope, Doi Sutep, 260 m, 15 July 1962 (WL 1.47 mm) and Khao-Yai National Park, 750 m, 26 July 1962 (WL 2.06 mm), E. S. Ross and D. Q. Cavnagaro. Malaysia: Pahang, below The Gap, about 850 m (R. H. Crozier), in hill forest. The MCZ also has a sample from Wai Lima, Lampong, S. Sumatra (Karny).

[10] The type of *P. nicobarensis*, a unique worker collected by the Galathea Expedition at Nancovri in the Nicobar Islands, is the same as an average *P. parallela* in size and nearly the same shape, except for the remarkable form of the head (fig. 37). HL 1.02 including clypeus, HW 0.73 (CI 72), ML 0.20 (from anterior point of clypeus), WL 1.63 mm. The head shape reminds one of some *Smithistruma* species in the myrmicine tribe Dacetini, with its deeply excised posterior border, ogival advanced free clypeal margin, and narrowly subtriangular (but apparently edentate) mandibles. The posterior clypeal border and the median frontal groove are indicated in fig. 37 by faint dashed lines; they are hardly this distinct in the specimen in most lights, and even the exact location of the posterior clypeal border is not entirely certain. The centers of the eyes are only slightly in front of the middle of the head length (distinctly in front of the midlength in *P. parallela*), and the scapes do not quite reach the posterior angles of the head; they could not be held straight back from their insertions.

The propodeal angles have small, blunt teeth, a little more prominent than those of *P. parallela*, the petiolar node is a trifle shorter and perhaps a bit more convex, with slightly more prominent posterior teeth, than is the rule in *P. parallela*, but these differences are so small that probably they will be found to be bridged by individual samples of the latter species.

The *P. nicobarensis* type is brown, opaque throughout, and covered by a fairly abundant pilosity of very short, fine, suberect hairs, including scapes and legs. Even in this pilosity character, the *P. nicobarensis* type is approached by some samples of *P. parallela* from the Ghats of Kerala State in S India.

It seems likely that *P. nicobarensis* represents a *parallela*-like stock that has speciated and specialized as an island isolate.

R. W. Taylor recently sent me a specimen from near Lac, Papua New Guinea, that is very similar to *P. nicobarensis*.

[11] *P. tricuspidata* is widespread in Malaya, Sumatra (type locality is Si Rambé), and Borneo. It is usually found running on large logs within or at the edge of rain forest, and the nests are probably in old beetle burrows deep in the wood. The ant runs very rapidly and is difficult to capture. Samples in MCZ are from North Borneo: Kiduk Arok, log in clearing, 4400 feet (Cambridge University Expedition, P. W. Bryant). SE Kalimantan: Pulau Laut, about 6 km E of Stagen dock, large log in low-elevation hill rain forest (W. L. Brown, Jr.). Malaya, Selangor: Ulu Gombak Forest Reserve, near tree lookout (R. H. Crozier). Sumatra: Wai Lima, Lampongs (Karny). The type of subsp. *penangensis* (type locality is Penang, Malaya) is a dealate queen. Wheeler distinguished it from the typical form, which he had not seen, by its significantly smaller size; actually, the *penangensis* type is 8.6 mm long, including mandibles, not "nearly 7.5 mm," as Wheeler gives it. It is about the right size to match most of the workers in the MCZ, and the fact that the Kiduk Arok worker is a little larger means little in this genus, in which size is so variable. Another character mentioned by Wheeler is the transverse rugosity on the propodeal declivity, which is fairly strong in the type of *tricuspidata* and some of the other worker specimens. But this rugosity is confined to the lower part of the declivity in all samples, and even in the *penangensis* type it is present in reduced form (and is not, as Wheeler claimed, replaced by delicate striation). In any case, the character is a variable one, and does not seem worth emphasizing. The proportions of the petiolar node, also cited by Wheeler, are just about what one would expect of a queen to go with the available workers of *tricuspidata*; at any rate, this character is again a somewhat variable one. There seems to be no reason to regard the *penangensis* type as representing a taxon separate from *tricuspidata*.

[12] *P. inermis* is a medium-small but robust species (WL 1.7–2.2 mm) that is apparently endemic to the Philippines. It can be recognized by its node, which is slightly higher than long, with continuously rounded anterior and dorsal faces, the latter rising slightly caudad, then steeply truncate behind, its posterior face usually feebly concave. In clean specimens, trunk, node, and gaster slightly shining. Antennae and legs brownish red in several series from the Cuernos Mts., Negros Oriental (J. W. Chapman), and in the type of the synonymous *maquilungi*, from Mt. Makiling near Los Baños, southern Luzon (C. F. Baker), but darker brown in samples from Baguio, Luzon (Chapman) and Trinidad, Samar (Chapman). See fig. 17.

Of *maquilungi*, Wheeler and Chapman (1925:123) say, "Resembles *P. inermis* Forel, but is smaller and has the posterior coxae toothed." However, Wheeler and Chapman give the total length of "6 mm," while Forel gives only 5.2 mm as the length of *inermis*. In any case, measurements were often wildly imprecise in those days, and the long series before me shows relatively slight size variation. The

"tooth" on the posterior coxae varies in distinctness from sample to sample, and even within nest series, and in some specimens is not evident at all, even when free of glue. The type of *inermis* was deposited in the Bureau of Science collection in Manila, and was undoubtedly destroyed with the building during World War II. There seems little doubt that *maquilungi* applies to a common variant of *inermis*. The type locality for *inermis* is Montalban Gorge, Rizal Province, Luzon (C. S. Banks).

[13] *P. clypeata* belongs to a poorly known group of rare species that includes also *P. gracillima* of Africa and probably *P. bidentata* n. sp., although the latter is more like the *P. sagei* group in the shape of the petiolar node. These species have gracile heads and bodies; long, stout antennal scapes; rather small, flat compound eyes; mesally convex clypeus; slit-shaped propodeal spiracles; unarmed propodeum; long, narrow petiolar node with sharp, strongly projecting posterodorsal margin that is shallowly (deeply in *bidentata*) emarginate mesad in dorsal view; and very fine sculpture relatively free of foveolae. The queen is known only for *P. clypeata*, and, like some other winged or dealate *Platythyrea*, it completely lacks ocelli. See figs. 23 and 24.

*P. clypeata* type (MHN — Geneva), an alate queen ("Pays du Moïs, Indochine") lacking the gaster: HL 1.37 measured from anterior clypeal margin, HW 1.00, ML 0.20, greatest diameter of eye 0.24, scape L 1.22, greatest scape W 0.21, petiolar node L 0.71, petiolar node W 0.43, WL 2.30 mm.

Posterior margin of head straight, very slightly concave mesad. Clypeus strongly convex in the middle, and the free margin rounded and projecting in the middle. Antennal scape held straight back from insertion surpasses posterior border of head by more than apical scape width when head is viewed full face. Sculpture and pruinosity exceedingly fine, integument feebly shining in some places, especially dorsum of petiole; larger punctures suppressed, nearly completely obsolete except on sides of petiole. Color brown with a slightly orange tinge, legs a little lighter.

The *P. thwaitesi* type (BMNH — London), also a queen ("Ceylon") with fore wing and hind wing present on the right side only, is larger than the *clypeata* type, has a relatively longer, lower petiole with posterodorsal angle not quite so sharp in lateral-view profile. In the proper light, one can with difficulty find small, shallow pits apparently corresponding to the ocelli, but the ocelli themselves are completely lacking, not just "weak," as Donisthorpe described them. Measurements: TL 8.7, HL 1.78, HW 1.23, ML 0.27, scape L 1.73, greatest scape W 0.24, greatest diameter of eye 0.33, WL 3.04, petiolar node L 1.13, petiolar node W 0.55 mm.

Despite the differences in size and petiolar proportions, I feel that *P. thwaitesi* should be regarded as a synonym of *P. clypeata*. These same characters are known to be variable in other *Platythyrea* species, and the resemblances shown

by the two type queens are impressive.

The palpi of these samples and of the *P. bidentata* types, described below, are of moderate length and can only partly be seen extending from beneath the closed labrum, in each case with 3 segments visible. It is thought that a fourth basal segment exists in each palp, to make a formula of 4.4 (as in *P. gracillima*, where a direct count is possible).

### *Platythyrea bidentata* new species

(Figs. 26, 28)

Holotype worker: TL 8.7, HL 1.77 (including clypeus), HW 1.33 (just behind eyes) (CI 75), ML 0.31, scape L 1.64, greatest scape W 0.26, greatest diameter of eye 0.30, WL 2.84, petiolar node L 1.10, W 0.57 mm.

Head with convex sides and transverse posterior border, very slightly concave, and the cervical margin of the head showing in full-face view. Frontal lobes convex, separated by a shallow, round-bottomed median sulcus that ends posteriorly where the lobes pass into the short, round-edged, parallel frontal carinae. Clypeus swollen and strongly convex in the middle in both directions, its free border with a narrow, rounded lamellar apron, broadest toward the middle. Posterior clypeal border fine but reasonably distinct. Mandibles robustly subtriangular, with very slightly convex outer borders and distinct teeth — a larger apical tooth, followed by alternating larger and smaller teeth, but all generally diminishing in size basad; 9 teeth visible, but there are probably one or two small teeth hidden beneath the clypeal margin. A short but distinct groove runs directly anteriorly from each mandibular insertion on the dorsal surface near the outer margin, and ends before reaching the outer margin. Eyes only feebly convex, sub-oval, situated exactly at mid-HL, covered with a pile of minute, erect hairs. Antennal scapes long and robust, thickest beyond midlength; in full-face view when held nearly straight back, surpassing posterior border by about twice their apical thickness. Basal funicular segment equal in L (0.35 mm) to III; segment II much the longest (L 0.50 mm), apical segment L 0.37 mm, weakly curved, with a flattened, narrowly rounded apex.

Pronotum as seen from above subcircular in its anterior  $\frac{3}{4}$ , without margins or humeral angles, separated from mesonotum by the usual distinct and flexible suture. Remainder of trunk with nearly parallel sides (slightly constricted in mesonotal region)  $\frac{3}{4}$  to  $\frac{1}{2}$  as wide as pronotum. Sutures between mesoscutum, mesoscutellum, and metanotum are nearly effaced but can be made out partly in certain lights as obscurely impressed marks. In side view, the dorsal outline is nearly straight from promesonotal suture to beginning of curve leading into propodeal declivity, except for a slight dip centered in the metanotal region. Declivity convex in side view due to low, bluntly rounded lateral margins; face of declivity subtriangular, concave from side to side, narrowed at the top and extending a short way onto the dorsal surface; indistinctly

transversely ruguloso-striate in the middle and lower parts. Propodeal suture distinct through most of its course, especially below the spiracles, which have slit-shaped orifices, about  $4\times$  longer than broad.

Petiolar node as in figs. 26 and 28, upper sides very shallowly impressed (concave) behind midlength, just in front of the bases of the posterodorsal teeth or lobes. Tergum of postpetiolar (first gastric) segment broader than long, rounded strongly in both directions in front, the rounded part overhanging the insertion. Sternum of postpetiolar segment also rounded in front, without process or ridge. Second gastric segment slightly longer, but slightly narrower, than first, but still a little broader than long. Pygidium narrowly rounded.

Legs long and robust; front coxae and femora especially well developed, the femur incrassate in the middle (maximum W about  $0.3\times L$ ); hind femur L 1.90, hind tibia L 1.56 mm. Tibial spurs 2 on each middle and hind leg, the lateral spur a little more than half as long as the inner one, all pectinate. Teeth of tarsal claw reduced and difficult to see, especially on first pair of legs.

Sculpture and pilosity of the usual *Platythyrea* kind; normally exposed surfaces of body, mandibles, and appendages very finely, densely, and shallowly punctulate and pruinose, with fine, short standing hairs on anterior clypeal margin, mandibles, and gastric apex. The surface is in general opaque, but a dull shine can be obtained in certain lights, especially from petiolar node and anterior sides of gaster. The larger punctures or foveolae normally found in *Platythyrea* are small and subdud in *P. bidentata*, but can be seen in the right light on the head, particularly mesad of the eyes, on the sides of the pronotum, and less distinctly elsewhere. Color very dark brown, appendages castaneous, shading into reddish yellow at the antennal apex.

Paratype worker: TL 8.4, HL 1.70, HW 1.23 (CI 72), ML 0.27, scape L 1.55, greatest scape W 0.25, greatest diameter of eye 0.26, WL 2.73, petiolar node L 0.91, W 0.53 mm.

Besides its smaller size and slightly smaller eyes, the paratype has a more distinctly impressed area in the region of the suture between meso- and metanotum, and the metanotum itself is slightly raised behind this. The paratype also has some coarse but only moderately distinct, prevailing longitudinal rugae on the posterior half of the middle sides of the petiolar node.

The holotype and the lone paratype both from the Cuernos Mountains, near Dumaguete, Negros Oriental, Philippines (J. W. Chapman), taken at an elevation of about 3600 feet. On the holotype locality label, "1942" is written on the underside in pencil, while on the underside of the paratype label is the pencilled date, "1/10/43." Holotype and paratype in MCZ.

*P. bidentata* is most closely related to *P. clypeata*, but the new species has a much more deeply excavated postero-dorsal petiole border, forming 2 blunt posterior teeth much



like those of *P. quadridentata*. The color of *bidentata* is also much darker than in the two known *clypeata* (including *thwaitesi*) specimens, both of which are isolated winged queens, and hence unlikely to be callow. *P. quadridentata* and *P. sagei* have blunt but distinct propodeal teeth, lacking in *bidentata*.

The *P. gracillima* type (AMNH — New York) measures: TL 10.7, HL 2.20 including clypeus, HW just behind eyes 1.56, ML 0.46, scape L 2.46, greatest scape W 0.30, greatest diameter of eye 0.31, WL 3.74 mm. Antennal scape surpasses posterior border of head by 0.94 mm when held straight back from insertion, full-face view. Palpal segmentation 4.4. Posterior border of head transverse, straight, except for very slight median concavity. Head widest near eye, tapering anteriorly and posteriorly. Clypeus convex, free border strongly rounded. See figs. 29 and 30.

Another specimen of *P. gracillima* has been received on loan from BMNH — London: Mampong, Ghana, 20 May 1970 (P. Room).

[14] *P. sagei* and *P. quadridentata* are closely related and form a group next to the *clypeata* group, and also near *P. bicuspis* of Madagascar. The *sagei* group has the propodeum as well as the petiolar node bluntly but distinctly bidentate. *P. sagei* (Belgaum) and *P. quadridentata* are readily separated by the characters given in the key (p. 10). So far as I know, *sagei* is found only in India. It has been reported (Viehmeier, 1916: 112) from Singapore, but this record could well belong to *quadridentata*, a variant of which is now known from North Borneo: Sungei Slau, one of 5 workers pinned with termite prey (HL 1.26, HW 1.10, WL 2.26 mm.), E Mjöberg; and Tabobon, 2950 ft., sandy ground near river, Sept. 1956, HL 1.18, HW 1.03, WL 2.10 mm), Cambridge North Borneo Expedition, P. W. Bryant, one worker. These workers have CI about 87, and greatest diameter of eye in these samples is 0.22–0.25 mm. The North Borneo workers differ from the Papuan ones collected by Wilson (1958b:152) in having the posterior petiolar teeth shorter and less acute, but the Tabobon specimen has fairly numerous fine, short (0.01–0.04 mm) erect hairs on dorsal surfaces, as in Papuan samples.

A *P. sagei* syntype from Belgaum, peninsular India (MCZ) has HL 1.30, HW 1.25 (CI 96), WL 2.47, greatest diameter of eye 0.37 mm. Belgaum is hereby selected as the type locality, since I have not studied the specimens from the other original locality, Dharmasala, N India.

[15] A *P. bicuspis* worker syntype from "Madagascar" (MCZ) has WL 3.52 and greatest diameter of eye 0.46 mm.; another worker specimen from Perinet, Madagascar, has WL 3.50, greatest diameter of eye 0.43 mm. In these workers, the second funicular segment exceeds in length the basal segment, and the basal segment is subequal in length to the greatest eye diameter.

[16] The 8 nominal species *turneri*, *tasmaniensis*, *bicolor*, *reticulata*, *septentrionalis*, *dentinodis*, *micans* and *brunnipes* make up the genus *Eubothropenera* in the sense of Clark. Clark himself did not include *turneri*, which was originally described in *Platythyrea*, and he did not recognize the close relationship of his genus to *Platythyrea*, thinking instead that it was related to *Pachycondyla* (*Bothropenera*) in tribe Poncini. Indeed, *Eubothropenera*, with its coarser sculpture, pubescence, and standing pilosity, and its high, broad petiolar node, looks quite a bit different from the usual hairless, pruinose *Platythyrea*. Nevertheless, once I had recognized the true affinities of *Eubothropenera* (Brown 1952), I found it difficult to separate it from *Platythyrea* on clear-cut characters. The erect hairs of *Eubothropenera* once seemed like a good discriminating feature, but now some *Platythyrea* species (e.g., *quadridentata*, *nicobarensis*) are known to have numerous short standing hairs. The broad petiole now seems like the best group character, but it does not look like a generic character.

The species of the *turneri* group, which I shall call it instead of "*Eubothropenera*," are very close among themselves, and it would not be surprising if they were all eventually to be put into a single species. All of them were originally described from restricted series, each from a single locality. As time went on, a few samples were added to the original ones, and the known variation of the species is seen to be broader than originally determined. I have now reviewed syntypes or paratypes of all of the 8 species except *brunnipes*, and I have also studied the additional samples mentioned individually below. My tentative conclusion is that only 3 species are distinguishable, and *P. brunnipes* is an insufficiently known fourth species that must remain doubtful until it can be restudied. Notes on the species are offered here *seriatim*:

*P. turneri*: This is the most widespread and variable of the species, if my synonymy is correct. It may be recognized by the coloration, in which the brownish red petiole always contrasts with the dark brown head and gaster; the trunk may be brown or reddish brown, but it is usually, at least in part, darker than the petiole. The types came from Mackay, on the central Queensland coast, and they are deposited in MHN — Geneva. I studied them briefly in 1963 but was prevented from reviewing them in 1973 because they had been held out on loan for several years by another specialist. Forel's original description and my own brief notes indicate that *turneri* is equivalent to Clark's *septentrionalis*, described from Townsville, N Queensland (MCZ), except that the median posterodorsal tooth of the petiolar node (a very variable character) is not developed in the *turneri* types. Additional samples from Queensland: Gladstone (F. H. Taylor) and the Kirrama Range, near Cardwell, 2000–3000 ft., eucalypt forest (P. F. Darlington) are very like the *turneri* and *septentrionalis* types in color and in having the coarse punctures prominent, the median petiolar carina developed, and the fine sculp-

ture of the head and trunk dense and opaque. See figs. 31-33.

Moving south, the next sample seen is the type series of *reticulata*, collected by W. M. Wheeler at Sutherland, New South Wales (MCZ). These specimens are less coarsely sculptured than are those of the Queensland species, but the difference is small. The next sample (MCZ) comes from Hobart, Tasmania (A. M. Lea), and is a syntype of *tasmaniensis*, which Forel had described in *Pachycondyla* (*Bothroponera*). This worker is essentially like *reticulata*, but has the ground sculpture still less dense, and consequently weakly shining, the larger punctures of the head indistinct, and the median tooth of the petiole reduced to nothing. Samples much like the *tasmaniensis* type have been taken in the area east of Esperance, in SW Australia: Merivale Downs, on tree trunk in yate (*Eucalyptus cornuta*) swamp (W. L. Brown); Thomas River Station, 110 km E of Esperance, in yate-paperbark-wattle forest (E. O. Wilson and C. P. Haskins), and a type of *bicolor* (MCZ), from Ludlow, still farther west in SW Australia, is still slightly more shining and has a feeble trace of a median petiolar tooth.

My interpretation of this admittedly sparse sampling is that a single species cline exists, with coarse sculpture in tropical coastal Queensland giving way to less coarse to the south, and then, jumping the desert gap, to the lightly sculptured southwestern populations. The species undoubtedly exists at many intermediate stations in S Queensland, E New South Wales, Victoria, South Australia and Western Australia, and when samples from these areas are studied, the clinal hypothesis for *P. turneri* will meet its proper test.

*P. dentinodis*: This species, still known only from the type series (MCZ) from Bungulla, Western Australia, is a unicolorous, yellowish red, or ferruginous yellow, described by Clark as "castaneous." The sculpture is rather loose and coarse and generally fairly strongly shining, and the middle of the posterodorsal petiolar margin bears a small but sharp and uptilted tooth. The standing hairs are dark, coarse and long, up to 0.18 mm long on some dorsal surfaces. The antennae, mandibles, and legs are no darker in color than the rest of the body.

*P. brunripes*, inadequately described by Clark from Reevesby Island in the Sir Joseph Banks Group, off the coast of South Australia, is also called "castaneous," a color term that Clark consistently used for tints of a much lighter color than is usually associated with that term by other authors. In fact, ants described as "castaneous" by Clark would usually be called "ferruginous" or "reddish yellow" by other authors. Clark said that the antennae, mandibles, and legs of *brunripes* were "brown," but his description of the sculpture and pilosity is so sketchy that we cannot say whether the species is related to *dentinodis* or to *turneri*; maybe it is to neither.

*P. micans* is a relatively delicately sculptured form, rather generally weakly shining and with very short standing

pilosity and tidy appressed pubescence, evenly dark brown in color throughout, from Western Australia. I have an additional specimen taken by E. O. Wilson and C. P. Haskins on the Mt. Ragged-Thomas River Track, sandplain east of Esperance, Western Australia, in mallee, 1955.

It seems to me that the treatment of the *turneri* group as only 3 or 4 species expresses the real relationship of the species better than did Clark's system, but we still need much more material in order to give the group a stable taxonomy.

[17] In the Americas, *Platythyrea exigua* and *P. zodion* are distinct, but the remaining species, forming the *punctata* complex or group, are both very close and highly variable, so that species limits are anything but clear. In fact, it is possible that most or all of these forms are variants, in part geographically distributed, of a single species that should bear the prior name *P. pilosula*. In this work, I have adopted a more conservative course, provisionally recognizing 5 species in the complex even though no one of them can be cleanly separated from all of the other 4. Let us consider each species in turn.

*P. pilosula* was not considered to be a *Platythyrea* before Donisthorpe made the new combination in 1932, so it was left out of discussions by Emery, Forel, Roger and others. I have reviewed the *pilosula* type (BMNH-London) from "Brazil," and find it very similar to type-compared specimens of *P. incerta*. Unfortunately, the impossibility of borrowing material from the Emery Collection in Genoa prevents me from comparing the types of *pilosula* and *incerta* directly, but I feel reasonably secure in considering the two synonymous after having looked at the type of *incerta* (MCSN-Genoa) and made notes on it in 1963. If *incerta* should happen not to be the same as *pilosula*, then it is most likely to belong to *P. sinuata*, which would take the name *incerta*, out of circulation anyway.

Measurements of *Platythyrea pilosula* holotype worker (BMNH-London) supplied by Barry Bolton: maximum diameter of left eye 0.36, minimum distance between left eye and mandibular insertion 0.31, L left anterior femur 1.34, maximum measurable W left anterior femur 0.46 mm; femur W/L is 34%. Basal mandibular groove absent.

*P. sinuata*, described from 2 workers and a male from Surinam (MNK-Berlin) was described by Roger as having the mandibles "sehr scharf gezähnt," but the type workers have the masticatory margin edentate and cultrate, as in the related New World species. Before I saw the types, I thought *sinuata* must be the slender form with grossly swollen fore femora, the most common species in the Guyanas and Trinidad, but instead they proved to be the species later described as *meinerti* by Forel. The form with swollen femora is believed to be *P. angusta*, although I have not studied the *angusta* type, because *P. angusta* is so far the only *Platythyrea* species known from Trinidad: (Nariva Swamp, N. A. Weber No. 138, 10 workers; Maracás Valley, Weber No. 438, 2 workers). Other samples

come from Guyana: Georgetown, separate series by H. O. Lang, W. M. Wheeler, and N. A. Weber; Kartabo (W. M. Wheeler); Dunoon (F. M. Gaige); Oko River, tributary of the Cuyuni (N. A. Weber). Venezuela: Caicara, R. Orinoco (G. K. Cherrie); Orinoco Delta and Ciudad Bolívar (N. A. Weber). Peru: Puerto América, Rio Putumayo (Cornell University Expedition, 1920); Puerto Bermudez, Rio Pichis (CUE 1920); Yurac, 67 mi. E. Tingo Maria (E. I. Schlinger and E. S. Ross); 10 km NW of Pucallpa (Schlinger and Ross). Ecuador: en route, Rio Bom Boisa (W. von Hagen).

The basal furrow of the mandible is very weak or absent in *P. angusta*, and the adult color of most specimens is black. The eyes of the worker are usually 0.30–0.33 mm in greatest diameter, about equal to the shortest distance from eye to mandibular insertion. The petiolar node is long and fairly narrow, with sinuate posterodorsal margin.

*P. meinerti* was originally described from La Moka, Venezuela. The type (ZMU – Copenhagen) resembles most clearly a specimen from 15 miles S. Santa Rosa, El Oro, Ecuador (E. I. Schlinger and E. S. Ross); it is conspecific with the *sinuata* types and a number of series in MCZ from Panama (Barro Colorado Island) and the Amazon Basin of Brasil: Belém, Pará (W. M. Mann), Pirelli Rubber Plantation, Iriboca, near Belém (W. L. Brown), Igarapé Marianil, 24 km N of Manaus, and Rio Tarumá, near Manaus (Brown); 20 km NE Manaus (W. L. and D. E. Brown). Peru: near Tingo Maria (W. L. Brown). Monson Valley near Tingo Maria (E. I. Schlinger and E. S. Ross). Guyana: Kurupung (H. O. Lang).

*P. sinuata* is usually fairly large (WL mostly 2.6 mm or more), and the workers are more commonly brown than black. The character usually associated with the species is the elongate petiolar node with the median tooth or lobe of the posterodorsal margin large, projecting and dominating the lateral teeth or angles, though the latter vary widely in size and acuteness from series to series. These lateral angles can be rounded and receding, or squared off, or acute and flaring. Another character of *sinuata* is the large size of the eyes, usually 0.40 mm in greatest diameter, or even more, though small-sized Panamanian specimens may have eyes as short as 0.30 mm. Usually, the eyes clearly exceed in length the distance between their anterior border and the nearest part of the mandibular insertion on the same side. The basal groove of the mandibular surface is typically distinct and runs to the lateral border, and the anterior femora are only moderately incrassate (W/L 30 to 34%). In one series (Rio Tarumá, near Manaus), however, the mandibular groove is variably indistinct, and the fore femora have a W/L ratio of 43–44%; in these respects the sample is more like *P. angusta* than *sinuata*.

The description of subsp. *boliviana* reads like *sinuata*, and this synonymy seems reasonable. *P. sinuata* is similar in size to *P. pilosula*, but tends to have larger eyes, a longer, less

rounded petiolar node with a more prominent median posterior lobe, and the strong basal mandibular groove, which is weak or lacking in *pilosula*.

*P. punctata*, the circum-Caribbean form, is relatively small (WL usually under 2.5 mm) and has a short, broad node, typically with sides diverging caudad and ending on each side in a strong, flared lateral tooth; median posterodorsal lobe or tooth usually low and gently convex, dominated by the lateral teeth. Basal groove of mandible usually strong and complete; anterior femora modestly incrassate (W/L about 1:3); eye 0.32–0.38 mm in greatest diameter, usually slightly longer than the distance from it to mandibular insertion. *P. punctata* differs from *P. pilosula* in its prevailing smaller size, broader petiolar node with dominant posterolateral teeth, and in having a distinct and complete basal mandibular groove.

*P. strenua*, the largest (WL 3.0 mm) and stoutest of the New World species, is isolated on Hispaniola Island, where it is known only from Mann's original collection at Diquini, Haiti. The eyes are about 0.50 mm long in 3 syntypes (MCZ), the mandibles have a very deep, strong and complete basal groove, and the anterior femora are only moderately incrassate. The petiolar node is nearly as broad as long, and the posterodorsal margin is dominated by a very broad, rounded median lobe that takes up more than half of the width of the border and is flanked by bluntly subrectangular lateral teeth. The low, gently convex dorsal face of the node meets the flat sides at a blunt angle that almost forms a dorsolateral margin on each side. The foveolae or coarser punctures are suppressed and indistinct in *P. strenua*, though a few can be seen on the vertex and sides of the petiole. The color is medium brown.

One of the structures showing maximal variation among species of this group is the petiolar node, particularly variation in length-width relationships and the shape and relative development of the teeth on the posterodorsal border. I have plotted length and width of the node in fig. 6 to include the available samples of the species *punctata*, *pilosula*, *sinuata*, and *angusta*. There seem to be 2 reasonably distinct regression zones: the lower zone belongs to *punctata*, while the upper zone contains mostly *angusta* at its lower end, mostly *sinuata* at its upper end, and *pilosula* extends widely through the middle and upper parts of the upper zone.

I have examined a few sets of *Platythyrea* male terminalia (fig. 131) from the New World, only one of which is definitely associated with workers in a nest series (Laguna Ocotal Grande, Chiapas, Mexico, 3 August 1954, R. L. Dressler). The species is *P. punctata*. The pygidium terminates in a slender, sharp, slightly downcurved spine. Other specimens (including one from Haiti assumed to be a male of *P. punctata*) show rather baffling variation, including 2 basically different types of parameres and 2 kinds of pygidia: one sharply spinose (*punctata* form), and one with the pygidium merely tapered to a narrowly rounded point.

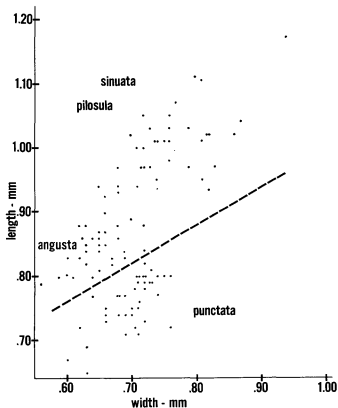


Figure 6. Scatter diagram shows length-width relationships of petiolar nodes of 105 workers and (a few) queens of 4 neotropical *Platythreya* species. Node length is greatest dorsal-view distance measured from anterior to posterolateral corners, ignoring median lobe or tooth, if present; width measured across widest part of node. Dashed line not a regression line but merely separates regression zone of *P. punctata* from those of the other 3 species. The latter overlap one another, but in general, *angusta* occupies lowest zone, *pilosula* upper middle, and *sinuata* highest.

Either 2-4 species are represented by these males, or else the terminalia of New World *Platythreya* species are extraordinarily variable. Only more material associated with workers can straighten out this tangle.

#### [18] *Platythreya zodion* new species

(Figs. 34, 35, 36)

Holotype worker: TL 4.9, HL 0.92, HW (behind eyes) 0.83 (CI 90), greatest diameter of eye 0.24, W across frontal lobes 0.47, scape L 0.54, ML 0.24, WL 1.56, fore femur L 0.75, fore femur maximum W 0.31 (W/L 41%), petiolar node dorsal view L 0.63, W 0.54 mm.

Shape of head, propodeum, and petiole shown in figs. 34, 35, 36. Note the broad convex mandibles with culate masticatory margins, apex of mandible subtruncate viewed end on; masticatory margin rounding evenly into basal margin. Basidorsal groove very fine, indistinct, not reaching lateral margin. Clypeus gently concave in the middle and with free margin medially concave. Clypeus not distinctly delimited from the frontal lobes, but the

frontal area forming a distinct pit that trails a shallow sulcus back to the center of the vertex. Eyes taking up approximately a third of length of sides of head, separated from antennal insertion by about 0.15 mm, or a little more than half the eye length. Undermouthparts closed, but palpi apparently with maxillary 6 and labial 4 segments (4 and 3 segments visible respectively); palpi short, in repose barely surpassing the posterior buccal border.

Antennae with pedicel very slightly longer than broad and very slightly longer than the succeeding (second funicular) segment; second segment very slightly broader than long; remaining funicular segments broader than long, except for apical segment.

Trunk robust, with a weakly convex dorsal profile as seen from side view, about  $2\frac{1}{2}$  times as long as broad seen from above, with rounded humeri and steep sides of pronotum, but not really marginate dorsolaterally. Sides of pronotum with an impression in posterior part. Promesonotal suture distinct, impressed, apparently flexible; metanotal groove obsolete, marked by a feeble impression at sides of dorsum. Mesopleuron distinctly bounded by complete sutures above and behind. Propodeal declivity concave, bounded by distinct margins that are especially prominent at the upper corners, but weak in the upper-middle portion due to a feeble median posterior impression of the dorsal face, seen best in oblique light. Upper part of declivity shining, very finely punctulate; lower part coarsely, transversely striate. Femur of anterior leg strongly incrassate—almost as strongly as in *P. angusta*.

Node well shown in figs. 34 and 35; note the lack of posterolateral teeth or angles and the faint vestige of a median tooth. Subpetiolar process rounded ventrally, with a small notch behind. Gaster with first 2 segments (postpetiole and true abdominal segment IV) about equal in width, with the second segment a little longer than the first, constriction between them moderately distinct. Sting robust, compressed.

Sculpture of the usual opaque kind in *Platythreya*, very finely and densely reticulate with fine, overlying pruinosity, the reticulation becoming more transversely elongate on gaster, and slightly more shining here. Coarse punctures abundant on vertex mesad of and behind eyes, but rather weak and inconspicuous. Coarser punctures on sides and posterior dorsum of trunk, on petiolar node, especially sides and anterior dorsum, and on dorsum of postpetiole. Fine, short erect hairs on mandibles, anterior clypeal margin, and gastric apex.

Color black; mandibles, antennae, and tarsi brownish yellow; tibiae and gastric apex dull yellowish brown; femora brown.

Holotype a worker from Ecuador: 2-8 miles N of Puyo, Pastaza (or Napo), about 950 m, 9 February 1955 (E. I. Schlinger and E. S. Ross), deposited in CAS—San Francisco.

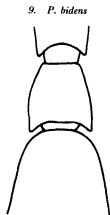
This species is distinguished from all New World *Platy-*



7. *P. bidens*



8. *P. procne*



9. *P. bidens*



10. *P. procne*

Figures 7-10. Two new species of *Probolomyrmex*, holotype workers, both from S India, petiole and adjacent structures in side view (7, 8) and dorsal view (9, 10),  $\times 73$ .

*thyrea* except *P. exigua* by its very small size. It differs from *exigua* by its much shorter head and virtually unarmed petiolar node. The node is also different in shape from those of all other neotropical species. The anterior femur is broadened almost as much as in *P. sinuata*, and the basidorsal groove of the mandible is present, though very fine. The type locality is in western Amazonian forest with small clearings, just out of sight of the Andes to the west (notes from E. S. Ross).

#### [19] *Probolomyrmex bidens* new species

(Figs. 7, 9)

Holotype worker: TL 2.7, HL 0.62, HW 0.41 (CI 66), scape L 0.41, WL 0.80, pronotal W 0.33, petiolar node L (from dorsal view) 0.31, petiolar node W 0.23 mm. Lateral petiolar index 83.

Similar to the other Indo-Australian *Probolomyrmex*, but a little larger and with a more robust body. Posterior corners of head more pronounced, more nearly rectangular, than in related species; posterior border straight, or even feebly convex in full-face view. No eyes detected at  $50\times$ .

In lateral view, the dorsal outline of the trunk is feebly sinuous from about the middle to the propodeal declivity; a slight tumulus marks the apparent position of the scutellum, and the first of 2 faint impressions behind it may represent the metanotal groove. Propodeal teeth fairly prominent, subrectangular, slightly better developed than in the previously described Indo-Malayan species (Taylor 1965:figs. 18, 21, 23).

Petiolar node special in form (figs. 7 and 9), with the sides ending behind in prominent triangular teeth. In dorsal view, the sharp posterior border is broadly excavated, but in the middle, the border shows the merest suggestion of a convexity that could be the vestige of a third tooth, developed to varying degrees in many species of *Platythyrea*, but not in any other species of *Probolomyrmex*. The subpetiolar process is like that of *P. greavesi*, but is even deeper, with the posteroventral corner a little less sharply angled. Postpetiolar (first gastric) segment robust, rounded in front as seen from above.

Exposed parts of palpi as in *P. damnermani*. Sculpture and pilosity as in other Indo-Australian congeners, but the larger punctures more numerous and more than usually distinct over head, trunk (especially pleura), and petiole; appressed pubescence also fairly distinct over most of body. Color dark ferruginous, legs and antennae a bit lighter, more yellowish.

Holotype a unique taken by Winkler apparatus (sample no. 27) in the Palni Hills, Madras State, India, 10 km NW of Kodaikanal, elevation 2150 m, 15 September 1972 by the team of Besuchet, Löbl, and Mussard of MHN—Geneva, where the type is deposited (Forel Collection).

The species is named for the paired strong teeth or angles of the posterior border of the petiolar node. In *Probolomyrmex*, such teeth are otherwise found only in *P. procne*, next described below, and also from the same region of southern peninsular India, but in that species, the node is much longer and has straighter sides, and the subpetiolar process is entirely different.

#### [20] *Probolomyrmex procne* new species

(Figs. 8, 10)

Holotype worker: TL 2.4, HL 0.58, HW 0.375 (CI 65), scape L 0.40, WL 0.75, pronotal W 0.29, petiolar node L

0.32, petiolar node W 0.21 mm. Head shaped much as in *P. dammermani*, *P. salomonis*, and *P. greavesi* (Taylor 1965: figs. 17, 20, 22) but posterior border less strongly concave even than in *P. greavesi* (Taylor, fig. 22). Although the head is narrow, the sides are convex. No eyes detected at 50 $\times$ .

Trunk (= Taylor's "mesosoma") much as in *P. salomonis* (Taylor, fig. 21), very feebly but evenly convex from front to rear in side-view outline, and propodeal teeth or angles a little better developed, almost rectangular. Petiole as shown in figs. 8 and 10, lateral petiolar index (see Taylor, p. 351) about 136, most like that of *P. dammermani*, but the dorsal surface convex behind as well as in front; seen from above with almost perfectly straight sides diverging caudad and ending in a pair of acute angles, with the posterior border between broadly and rather deeply concave. In the 3 previously described species, the node is shorter and has distinctly convex sides as seen from above, and the posterodorsal border is rounded (feebly emarginate in the middle in *salomonis*) or transverse and nearly straight (*greavesi*).

Postpetiole (first gastric segment, or true abdominal segment III) fairly robust, as in *greavesi*, but truncate anteriorly.

Maxillary and labial palpi, as much as can be seen of them, as in *P. dammermani*. Erect pilosity restricted to a few hairs on the mandibles; sculpture-pubescence of the very fine, opaque "pruinose" kind (50 $\times$ ), overlain by larger punctures of foveoleae that are particularly distinct on the 2 main gastric segments, where the integument is slightly more shining; the sculpture is like that of *P. dammermani*, except that the larger punctures are a little larger and more distinct on node and gaster. Color medium ferruginous (or "golden-brown" in Taylor's parlance) with more yellowish antennae and legs.

Holotype worker a unique taken by Winkler apparatus (sample no. 20) in the Palni Hills, Madras State, India, 39 km E of Kodaikanal, elevation 650 m, 11 November 1972 by the team of Besuchet, Löbl, and Mussard of MHN—Geneva, in which institution the type is deposited (Forel Collection).

*P. proce* is named after the mythical woman who was changed into a swallow, and hence the swallow itself, because of the dorsal-view shape of the petiole in the ant. This petiolar form will readily distinguish the species from all others in the genus. The subpetiolar process is like that of *P. dammermani* and unlike that of *P. bidens*.

[21] A single worker taken in rain-forest leaf litter berlesate at the Quebrada Susumuko, 1000 m, 23 km NW of Villavicencio, Meta, Colombia (S. and J. Peck, B-234) is considered to belong to *P. petiolatus* after direct comparison with the type (Weber Coll., now in MCZ). The new specimen has TL 2.6, HL 0.63, HW 0.39 (CI 62), scape L 0.40 (SI 103), WL 0.83 mm, and the lateral petiolar index of

Taylor is about 94 (vs. 85 for the *petiolatus* type, although I find the node measurements as defined by Taylor somewhat ambiguous). Thus, the Colombian specimen is larger, has a longer, relatively narrower head, and longer scapes than does the *petiolatus* type, and its petiolar node is a little longer; also, the posterodorsal margin of the node is a little more deeply concave (as seen from above) than in the type. The larger punctures of the gaster are more distinct than in the *petiolatus* type, and the subpetiolar process has the posteroventral corner drawn out into a sharp, caudally directed spur. The color, medium ferruginous with more yellowish appendages, is a little darker than that of the type.

Considering the variation now known to occur within such species as *P. dammermani*, *P. petiolatus*, and *P. guineensis*, the formal synonymy of *P. angusticeps* and *P. boliviensis* (Taylor 1965:360–363, figs. 30–33) seems due, and also the synonymy of *P. parvus* under *P. brevisrostris* (Taylor 1965: 355 gives sufficient evidence for this).

[22] Collections of *P. guineensis* workers have now been made in Ghana: Legon, on ground, 15 July 1970 (D. Les-ton); and Ivory Coast: Lamto Research Station, SW of Toumodi (J. Lévieux). These show slight variation in overall size, in length of petiolar node, and in sharpness of the posteroventral angle of the subpetiolar process.

[23] The *Cerapachys* of the Indo-Australian region include many — certainly more than a hundred — distinct species, described and undescribed. Nearly half of them are Australian species formerly assigned to *Phyracacae*, *Neophyracacae*, and *Lioptenera* — all with petiolar nodes sharply margined on the sides. In Australia, this contingent has prospered greatly, and has radiated to produce several stocks, including some in which the lateral margination extends to the trunk, to the postpetiole, and even to the postocular sides of the head. The radiation also involved color, so that species occurring in the more xeric habitats are predominantly light red, while those from cooler and wetter forested situations in the east and in southwestern Australia tend to be black, with mixtures of colors and exceptions in intermediate zones. There evolved a group of medium- and large-sized red forms, in which the functional workers of each colony all have 3 ocelli; this is the grassland-arid-country stock called *Neophyracacae* by Clark (1941).

*Phyracacae*-like species were not discovered in Australia until 1895, and the real flood of descriptions of new species only started slowly in 1910–1915, but rose with Wheeler's 1918 paper, and overflowed in Clark's papers of 1923 to 1941. The papers of Wheeler and of Clark added greatly to our knowledge of the biology of the Australian species, but they also added a long list of ill-defined forms, particularly in the medium- and large-sized species-groups of *Phyracacae* and *Neophyracacae*. Clark never provided a key to replace the already weak one of Wheeler (1918), even

though he nearly trebled the number of species recognized by Wheeler, and Clark's descriptions and figures are often so maddeningly indefinite and crude that only a generous representation of his syntypes, "paratypes," and other material in MCZ labeled as various kinds of types, gives us some idea of his concept of these species.

I have been able to study properly types of a majority of the nominal Australian species with marginate petiole, but a number of the species are based on uniques or only a very few specimens, which were not available to me for study. Nevertheless, I believe that most of the widespread and common Australian *Cerapachys* are now described, and a species key should prove helpful in organizing the eventual revision that will be done by an Australian worker able to see the types and additional material accumulated on that continent. Where differences between species are not clear, I have simply run the names out together.

The situation in the Indo-Malayan region is even less satisfactory than it is in Australia. Most of the species known from Melanesia and westward belong to the *dohertyi* group, still unrecorded from Australia, but there are also some in the *Phyracaces-Lioponera* (*pubescens*, *suscitatus*, and *longitarsus*) groups. At least a dozen undescribed new species now in collections are known for the Indo-Melanesian area, even after the descriptions contained in this paper are counted. Some of these novelties are Philippine species gathered by J. W. Chapman, in such poor condition that they cannot be confidently described; others are from India, Borneo, New Guinea, and other places, but always in disadvantageous sample sizes, or else they belong to such difficult groups that they cannot be confidently described without our knowing much more in general about within-species variation, particularly allometric variation, in the *Cerapachys* of this region. In addition to these, there are undoubtedly many new species as yet uncollected, judging from the rate at which new forms keep turning up. Even some of the described species (e.g. *bakeri*, *salimani*, *conseratus*) are so poorly known that they must be placed in the key largely on guesswork. This discussion is by way of warning to users of the key. Obviously, the key must be regarded as only a very incomplete sketch of what more advanced revisions will allow, and identifications made with its help should be checked with reliably identified material.

The user should also be warned that in this genus, separation of worker and queen castes is cursed with unusual difficulties. Ergatoid queens of various grades, usually with 1 or 3 ocelli, may occur in species that also have (or lack) winged queens. In some species, all functional workers have 3 ocelli. Isolated specimens with a workerlike habitus often should be regarded as ambiguous castewise until nest series can be found with the different castes represented.

[24] *C. crawleyi*, with its remarkable costate sculpture, was the basis for Crawley's concept of the genus *Chrysapace*.

Crawley (1924:380) included the single species *jacobsoni* Crawley in his new genus, but when Wheeler (1924:225) suggested that *Chrysapace* was merely a subgenus or synonym of *Cerapachys*, *jacobsoni* Crawley became a conditional homonym of *C. jacobsoni* Forel [25]. Wheeler mentioned 2 substitute names for the species: *mirandus* and *crawleyi*, though it is reasonably clear that he actually meant to apply only the latter in a formal way, and as first subsequent reviser, I choose *crawleyi* as the prior name.

There are available so far as I know 5 specimens of *C. crawleyi*: the type (BMNH—London), a worker (not a queen) from Suban Ayam, Sumatra; another worker from Wai Lima, Lampong, S Sumatra (Karny) in MCZ; 2 workers (MCZ) from Camp Lookout in the Cuernos Mts., near Dumaguete, Negros Oriental, Philippines (J. W. Chapman, no. 1136); and an alate queen (BMNH—London) shown in figs. 48 and 49, from Mt. Matang, Sarawak.

The alate queen from Sarawak measures: TL 9.8, HL 1.55 (excluding frontal carinae), HW just behind eyes 1.64, scape L 1.30, greatest diameter of eye 0.43, WL 2.76, L petiolar node, sculptured part, dorsal view 1.26, petiolar node W 0.94, postpetiole L, side view 1.20, forewing L 5.8, left hind femur chord L 1.43, left hind tibia L 1.10, left hind metatarsus L 0.94 mm. CI about 92, petiolar node W about 75% of L.

The Wai Lima worker has petiole L 1.19, W 0.83 mm, so that W is about 70% of L; entire trunk with curved transverse costae, the convexity of the curves posteriad. Propodeal declivity flattened, without lateral or dorsal margins, but finely pubescent. Both nodes and gaster longitudinally costate, the costae of the first gastric segment (true abdominal segment IV) diverging slightly caudad.

The two Philippine specimens have shorter petioles: L 0.85, W 0.73 and L 0.81, W 0.72 mm respectively, so that W is 85% and 89% of L in these two workers. The propodeal declivity is clearly margined laterally and above by a semicircular carina, and the first gastric segment in one specimen has longitudinal costae diverging slightly behind, while in the other specimen, the costae are arched over a small posteromedian parcel of longitudinal units. The costae on the truncal dorsum are curved-transverse (as in Sumatran specimens) posteriorly, but change to longitudinal and anteriorly diverging on front half of trunk.

Crawley's type worker has petiole 0.84 mm long, 0.74 mm wide (W 88% of L), and the propodeal declivity has a distinct raised margin above and on the sides, like the Philippine workers and the Sarawak queen, *teste* B. Bolton *in litt*.

The Taiwanese species *sauteri* is not available for examination, since the whereabouts of the Sauter Collection at present is unknown to me, but Forel's description indicates that this species may belong to the *crawleyi* group. Forel's description of the costulae on the head is difficult to interpret, but at least this sculpture sounds different from what I see in the *crawleyi* specimens. Forel also says that the mandibles are "schwach lederartig gerunzelt" (finely

striate in *crawleyi*) with scattered coarse punctures, and apparently the trunk in *sauteri* is longitudinally costate. The smooth but punctate gaster seems like an unequivocal species character. Forel says nothing about the tibial spurs; a larger medial and smaller lateral narrowly pectinate spur occurs on each tibial apex of the middle and hind legs in all *crawleyi* specimens seen.

[25] The group of *C. antennatus* contains 9 nominal forms from the mainland of Asia, the larger islands of the Sunda Shelf, and (at least) the central Philippines. These are black species with 12 antennal segments, the apical segment dominant, but not grossly thicker than the rest of the antennae; that is, intermediate between the condition of most *Cerapachys* species and those that have been called *Phyracces*. The integument is predominantly smooth and shining, usually with a bluish opalescence, except for the petiolar node, which is coarsely costate or foveate save for a shining median longitudinal sulcus or strip. The petiolar node and the body form in general are also somewhat intermediate between the "usual" *Cerapachys* pattern and that of *Phyracces*; in fact, the species *vandermeermohri* was even described as a *Phyracces* originally. It is well to bear in mind, though, that *C. antennatus* of this "intermediate" group is the type species of *Cerapachys*.

I have now reviewed the types of 8 of the 9 nominal species, plus some very revealing additional samples, and the first rough sort groups the species this way:

- A. *jacobsoni* Forel (not *Crawleyi*) Java  
*jacobsoni sumatrensis* Sumatra  
*vandermeermohri* Nias I. off Sumatra
- B. *sulcinodis* Burma  
*risi* Hong Kong  
*butteli* Sumatra
- C. *antennatus* Sarawak  
*wheeleri* Sarawak
- D. *manni* Sumatra, Borneo

The species of set A are very similar among themselves, and also match well samples from E Kalimantan; 31 km N of Balikpapan, rainforest (W. L. Brown); North Borneo, Mt. Poi (E. Mjöberg); Philippines: Cuernos Mts., Negros Oriental; Malaya: Fraser's Hill (R. H. Crozier).

The samples are all so small (1–6 workers each) that we cannot say much about intracolony size variation, but among these samples at least, size variation is moderate (petiolar node L 0.67–0.75 mm, N = 12 individuals). These workers have the space between the eye and the mandibular insertion smooth, with only a few scattered punctures, and the line of the metanotal groove is weakly impressed all the way across the truncal dorsum. There are slight differences in the width of the anterior part of the postpetiole, and in the form of the rim that runs around it, but I believe it is reasonably clear that set A represents a single morphospecies with the prior name *C. jacobsoni*.

The species of set B are similar to *C. jacobsoni*, but vary greatly among themselves in size and in characters, both allometric and otherwise. All of the set B samples have a

groove or connected chain of punctures connecting the circumcircular groove with a ridge along by the mandibular insertion. Sometimes this groove and the raised seam accompanying it are part of a field of 2, 3, or more irregular rugulae stretching between the eye and the mandibular insertion. Workers with such a cheek groove also tend to lack the metanotal groove, or have it suppressed to the point where it is represented at most by a transversely elongate median puncture, but this character is somewhat variable and is best seen by direct comparison with *C. jacobsoni* workers.

We now have available, in addition to the types of *sulcinodis*, *risi*, and *butteli*, 5 samples of one to a few individuals each: China, S. Kiangsi Province, Hong San (J. L. Gressitt); Sikkim: Sundukphoo, 12,000 feet (Col. Bingham); North Borneo: Trus Madi Massif, 4600 feet (P. W. Bryant); Thailand: Doi Sutep, 110–1275 m (E. S. Ross and D. Q. Cavagnaro); Philippines: Cuernos Mts., Negros Oriental, 1100 m (J. W. Chapman). More important, we also have a very large series, originally containing several hundred workers from Thailand: Doi Sutep (Mt.), 260 m (Ross and Cavagnaro).

The Doi Sutep sample of 8 individuals includes some of the largest and smallest individuals I could pick out of hundreds. The small workers are similar to those from Sikkim, but the largest individuals have markedly broader heads, larger eyes, 3 well-developed ocelli, a slight tendency toward development of dorsal truncal sutures, and peculiar, wide petiolar nodes (e.g., L 0.75, W 0.89 mm; L 0.80, W 0.85 mm; L 0.85, W 0.93 mm for 3 specimens). The petiolar nodes are also peculiar in having the usual longitudinally costate dorsal sculpture "stretched out" laterally into a broad flat or feebly concave, or even feebly convex, median smooth area flanked on each side by a belt of coarse, confluent punctures or foveae along the lateral margins. One sees that the narrow median sulcus of smaller workers (and *jacobsoni*) is homologous to the wide median area of larger specimens, and also of the larger *C. manni* (set D), which is known only from winged or dealate "perfect" queens (e.g., 2 examples from 3000 ft on Mt. Dulit, N. Borneo, E. Mjöberg). Whether the large ocellate individuals are to be classed as "ergatoids," and whether they are reproductives (perhaps supplementary to or replacing a normal queen), are open questions. The Chinese specimen from Hong San is interesting in this regard; its petiolar node is intermediate in length (L 0.77 mm), but very wide (W 0.91 mm); the pterothorax shows some division into sclerites, but wing stumps are lacking; the ocelli are present, but the 2 posterolateral ocelli are reduced.

I am certainly tempted to consider the set B samples as the workers and ergatoids of one species (*sulcinodis*), the perfect queens of which are represented by *Crawley's C. manni*. A complication exists in the form of a smaller winged queen (MCZ) from North Borneo: Trus Madi Massif, 4400 feet (P. W. Bryant), petiole L and W both



0.65 mm, and petiolar sculpture costate, more as in small workers of other series.

Next to be considered is the worker type of *C. antennatus* itself (set C). This specimen (BMNH—London), from Sarawak (A. R. Wallace), is in the size range of the larger *sulcinodis* (trunk  $L_s$  or  $WL_s$  about 1.86 mm; petiolar node 0.82, W 0.73 mm), and the antecular cheek has a longitudinal groove paralleled by 2–3 more rugules in front of this, but the metanotal groove is present and complete, if weak. The petiolar node has a smooth, convex disc with scattered punctures, but the sides of the node near the top are coarsely, confluent punctate and form an irregular groove and ridge at the dorsolateral margin on each side, continuing a sharp anterodorsal margin and a weaker one behind. The node, though convex discal, is more or less depressed and *Phyracaces*-like in form. It is also not hard to view it as a relatively modest (intermediate?) variation of the *sulcinodis* patterns of worker and “ergatoid” described above.

Crawley (1926:387–389) published a redescription of the *C. antennatus* type, and Wheeler (1919:45) had already published one of what he thought was the worker of *Cerapachys antennatus* from a specimen taken by Hewitt at Kuching, Sarawak. Crawley (1926:389) discussed Wheeler's specimen, briefly advancing reasons why he thought it could not be the same species as the type of *C. antennatus*, and ended by offhandedly proposing for it a new species (*C. wheeleri*) in the text of his paper. Crawley never himself saw the specimen in question, and no one can now say whether it was ever labeled as type of *C. wheeleri* after having been in fact made a holotype in this obscure fashion. Unfortunately, the specimen now has been lost.

Wheeler's collection was divided between MCZ and AMNH—New York after his death, and later a number of individuals and institutions made selections from the MCZ part of the collection for their own uses. It is to be regretted that much of the original Wheeler material was thus dispersed in a relatively casual way, without knowledge of, or regard for, the possible critical significance of particular specimens or series. Ant taxonomy has suffered subtly but seriously from this dispersal ever since Wheeler's death, and the present instance of the loss of a crucial type specimen is only one example of the general problem.

I have checked the AMNH—New York, BMNH—London, and USNM—Washington, as well as MCZ, but the curators of these collections could not find anything that might be the type in question. There are perhaps still collections to be searched (for example, the W. S. Creighton Collection), but as this is written, conditions prevent a further investigation of the matter.

In considering carefully both Wheeler's description and Crawley's remarks, and after personally reviewing the type of *antennatus* in London, it seems to me that Wheeler was probably right in ascribing the Kuching specimen to *C. antennatus*. Crawley (p. 389), in describing the *antennatus* type, makes a point of writing: “There is no trace of longi-

tudinal grooves on the petiole, as in *sulcinodis* Em., and *jacobsoni* For., nor of any confluent punctures as stated by Wheeler...”

But, as I have already mentioned in my note (above) on the *C. antennatus* type, the confluent punctures on the sides of the petiolar node near the top are really there. The additional characters cited by Crawley for *C. wheeleri* do not seem of much consequence, since all are variable in this species-group, and in any case, Crawley saw them only through Wheeler's description. In view of the fact that the *wheeleri* type is missing, it seems to me that the most direct solution to this problem is to yield to the probability that *wheeleri* belongs to the same biological species as *antennatus*. Following this course, I have placed *wheeleri* as a junior synonym of *antennatus*.

The *C. manni* (Set D) queen is massive. A specimen from Mt. Dulit in northern Borneo has the apical antennal segment L 0.78, W 0.33; penultimate segment W 0.30. Petiole flattened above, marginate in front and weakly on sides. Frontal carinae close together, almost fused, but only raised about 45°. Eyes near midlength of head, slightly closer to back than to front. Claws all simple and slender. Tibiae all with a single large pectinate spur.

It is my feeling that further sampling will eventually hook up *sulcinodis* (set B) and *manni* (set D) with *antennatus* (set C), and show that they are all variants of a single species in which the “allometric size threshold” allowing a worker-ergatoid queen polyphenic spread, versus worker-queen and possibly worker-ergatoid spreads, varies considerably between series. Alternatively, it is possible that the pie should be cut so as to apportion species with similar (smaller) workers to different reproductive modes, viz. “small-queen,” “large-queen” (*manni*), and “ergatoid” species. I have somewhat arbitrarily decided to recognize the 4 sets A, B, C, D as separate species for the present, while realizing that all of them, even set A, may eventually be considered as variants of a single species to be called *Cerapachys antennatus*.

[26] The type of *Cerapachys oculatus* is a male myrmicine, but it does not belong to tribe Basicerotini, where previous conjecture has placed it. This male has long, protruding genitalia, somewhat like those of *Myrmecaria* spp., but the petiolar node and the junction between postpetiole and gaster are aberrant. The head is elongate, squarish, and depressed, with large eyes situated forward and large ocelli. The middle and hind tibiae are without spurs. I do not know this genus, but it might possibly be the unknown male of *Acanthomyrmex*. At any rate, it is certainly not a cerapachyine.

[27] *C. foreli* is widespread in western and central Africa. It is a black species with eyes occupying about 1/3 of the sides of the head; the head itself is rather wide and has a transverse (usually slightly concave) posterior margin with rounded corners as seen in full-face view. Wheeler's fig. 4 is incorrect in showing this; evidently the back of the head there was drawn while the head was tilted for-

ward, and not in the full-face position seemingly represented. The trunk is closely costulate along its whole dorsal length, and the petiole and postpetiole are covered with coarse, crowded, often elongate punctures. The gaster is densely covered with finer, round punctures separated by smooth spaces, much as in *nkomoensis* and *suscitatus*. The head behind has coarse punctures that in some cases form lines with indistinct costulae between, running forward to near the eyes, but this is a variable character.

I have not seen the type of *foreli*, which evidently is in the Silvestri Collection at Portici, but Santschi's description and his later (1915) figure of the petiole fit well enough the samples of the species from western Africa now available: Dabou Savannah, 47 km W of Abidjan, Côte d'Ivoire, 18 Jan. 1963 (W. L. Brown), 3 workers running up tree trunk in a copse within tall grass savannah. Tafo, Ghana, 26 Nov. 1970 (B. Bolton), log mold. Nimba Mts., Guinea, about 1000 m (M. Lamotte), forest, type of *occipitalis*. These workers average considerably smaller than the few central African ones at hand. The smallest Ivorian worker has WL 0.99 mm, whereas a Congo specimen (Lubila) reaches WL 1.20 mm and seems to be at least twice the bulk of the smaller one. Nevertheless, there is broad overlap between western and central African series in size, and the smallest Congo specimen, Epulu (E. S. Ross and R. Leech) is no bigger (WL 0.99 mm) than the smallest Ivorian worker.

A clearer difference between western and central African samples is that portrayed, evidently in a somewhat exaggerated way, in Santschi's 1915 figures. The petiole of the western specimens has the posterolateral angles produced as flat, acute, often somewhat incurved teeth; whereas in the Congolese samples, the teeth are often smaller and scarcely projecting, i.e., more nearly rectangular. The size and shape of these teeth, however, varies in both regions. There are also differences in length-width proportions of petiole and postpetiole, but actual measurements of these elusive traits shows that they are not very important and are, in part, geometric illusions due to differences in position, etc.

Wheeler differentiated *langi* from *foreli* partly on the basis of size and petiole shape, but in view of the foregoing discussion and the impressive overall similarity between western African and Congolese samples otherwise, I consider these as at most regional differences within one species. Wheeler's cited difference between *langi* and *foreli* in occipital shape is based on a false idea of his own *langi* types, and the scape length and sculpture differences, based only on Santschi's description, do not seem real in the light of the new material here considered.

Wheeler also proposed the name *santschii* for the queen figured by Santschi in 1915, again without seeing the actual specimen. I have compared the *santschii* type directly with syntype queens of *langi* and consider them to be the same, despite a small size difference. Other specimens from the former Belgian Congo (currently Zaire) are: 26 miles

S of Uvira, 800 m, 10 Jan. 1958 (E. S. Ross and R. E. Leech); Reserve Floristique de Yangambi, 29 March 1949 (A. Raignier and J. van Boven, No. 2231); plus the specimen already mentioned above from Epulu.

The type of *occipitalis*, very crudely described and figured by Bernard, has been examined and is not significantly different from the other West African samples or from Santschi's original description of *foreli*. Bernard underestimated the eye size in his type of *occipitalis* (in his fig. 6E, eye size is more nearly correct, but the shape is off).

Very closely related to *foreli*, and possibly even conspecific, are the types of *Phyracaces cooperi* Arnold and *P. vespula* Weber. Essentially, these forms are *foreli* with the costulate sculpture effaced over most of the truncal dorsum and replaced by a smooth, shining surface with scattered coarse punctures. At the anterior and posterior ends, the truncal dorsum has short zones of longitudinal costulae corresponding to the ends of the continuous costulate sculpture of *foreli*. In fact, even in the limited material seen, the extent of this costulate sculpture varies, and it would not be surprising eventually to find clinal variation connecting the two species in east-central Africa. It seems best for now to recognize two species, *foreli* being one. The other is represented by *P. cooperi* and *vespula*; I cannot separate these last two, and consider them as subjective synonyms. As first reviser, I indicate *Cerapachys cooperi* Arnold, 1915: 14 to be the senior homonym of *Phyracaces cooperi* Arnold, 1915:18 as now included in the genus *Cerapachys*. *Cerapachys vespula* is the next available name for the smooth-backed form, and is here so applied.

The name *cooperi* appears a third time as a homonym because Donisthorpe's *Lioponera cooperi* is now placed with the rest of the *Lioponera* species in *Cerapachys*. This problem is discussed elsewhere [33]. The confusion over these three homonyms seems to have been resolved by the suppression, one way or another, of all three epithets "*cooperi*," because the senior homonym is a subjective synonym of *C. afer*.

Syntypes of *C. afer* (worker) and *C. cooperi* Arnold (I) in the Forel Collection compare very well in form of petiole and postpetiole, color, and sculpture. It is clear that Arnold, when he described *C. cooperi* in 1915, simply left *C. afer* out of consideration because the *afer* types came from E instead of S Africa.

[28] According to his original description, Forel received the unique worker types of *Phyracaces nkomoensis* and *P. cooperi congolensis* from Kohl, who collected them at St. Gabriel, former Belgian Congo. In fact, they bear accession or collection numbers "202a" and "202" respectively, and they are so similar that they may well have come from the same colony. As I found the type originally, *P. nkomoensis* was very dirty and half-buried in old glue. When partly cleaned up, the supposed differences from *congolensis* disappeared. I cannot say anything about the differences cited by Forel except that they are either nonexistent or overstated by that author. Key measurements are for

*nkomoensis* type: WL 1.20, petiole W 0.63, postpetiole L 0.60, postpetiole W 0.66 mm; for *congolensis* type, WL 1.05, petiole W 0.61, postpetiole L 0.55, postpetiole W 0.63 mm. *P. eidmanni* holotype (Fernando Po) differs in larger size and slightly longer postpetiole, but is otherwise very similar: WL 1.45, petiole W 0.68, postpetiole L 0.74, postpetiole W 0.74 mm.

[29] The type worker of *C. braunsi* in the Emery Collection is small, blackish piceous, with very large eyes taking up half of the sides of the head. Head almost circular in full-face view, with the convex eyes making up a large part of this outline. The eyes are peculiar, almost reniform, in shape as seen from the side, with the ventral margin straight or even feebly concave. Petiolar node also peculiar, with strongly rounded sides passing into broadly rounded posterior lobes separated by a broad and deep concavity. Postpetiole considerably broader than petiole, with strongly rounded sides passing into a convex posterior border, so that it is subelliptical in outline. The type is from Willowmore, Cape Province, in the center of the arid Karroo country.

[30] The group of *C. cribrinodis* includes 12 nominal species of small (TL 2.6 to about 6 mm), reddish brown to black forms occurring in widely scattered parts of Africa S of the Sahara. The sculpture of all these basically consists of smooth or nearly smooth head, trunk, and gaster, with punctures varying according to the species from few, minute, and sparse, to many, coarse, and crowded. The nodes of the petiole and postpetiole may be sculptured much like the trunk, or one or both nodes may have a much coarser and denser punctation. The eyes are usually fairly large and convex, taking up a fifth to a quarter or so of the sides of the head, and situated near or at the midlength of the head. The node varies in shape from slightly longer than broad in *C. centurio* n.sp. [31] from Zaire, or barely broader than long in the South African *C. peringueyi*, to considerably (1¼ times or more) broader than long in *cribrinodis*, *afra* [27], *natalensis*, *sudanensis*, *validus*, and *faurei*. Probably *C. arnoldi* is like *C. peringueyi* in petiolar form; *C. villiersi*, though Bernard gives no information on the point, is apparently so much like *afra* and *sudanensis* that we may guess that the petiolar node is broader than long. The posterodorsal margin of the petiolar node is sometimes what Arnold called "bisinuate," that is, there is a slightly raised and feebly protruding median portion, flanked on each side by a weakly concave part, and outside this on each side a rather prominent (often sharply rectangular) posterolateral angle, especially as seen from a view a little in front of and above the node. This formation is most distinct in *C. afra*, but can be seen also in *sudanensis* and *natalensis*, and probably occurs also in *cribrinodis* and some other species.

For the present, I do not feel able to complete a revision of this difficult group. In the first place, the material is

much too scanty to deal with species that are obviously similar and at the same time very variable. Both allometric and nonallometric variation affect the sculpture (size and density of punctures) and form of petiole and postpetiole in this and some other *Cerapachys* groups, within as well as between nest series. Most of the species are known from one or two partial nest series, and in some cases (*validus*, *villiersi*) from unique type workers that I have not been able to examine. I doubt strongly that more than 7 or 8 (perhaps fewer) real species are represented by the 12 names left in this group. Particularly suspect are *C. arnoldi*, which may be only a variant of *C. peringueyi*, and *C. villiersi*, which was never satisfactorily distinguished from, e.g., *sudanensis* and *afra* in the first place. I have summarily synonymized var. *latiuscula* of *peringueyi*, and var. *hewitti* of *arnoldi*, because I believe that they are only allometric size variants of their respective species. *C. faurei* could well be only a small variant of *afra*, but I have not seen the types. *C. validus*, a black form with the head about as broad as long, according to the description, is a high-altitude grassland form from the Drakensberg Mts. of Natal.

In addition to the species discussed, I have seen material from Zanzibar (BMNH) in which the workers have much smaller eyes (about 10 facets only) than is usual in the group. There is also a large, coarsely sculptured, reddish brown form, *C. centurio* n. sp. [31], with the petiolar node slightly longer than broad, that has been taken at least 3 times in what is now Zaire. This form apparently has been misidentified as *cribrinodis* by Wheeler and by Arnold, at least. I have foregone formal descriptions of a few probably new species in favor of the future reviser of this group, who hopefully will have much more material and all of the types at his disposal. It should be pointed out that *C. sylvicola*, *C. lambornii*, and *C. kenyensis*, although they were keyed out separately from the *cribrinodis* group, are probably best considered as its members.

I have compared a worker syntype of *C. variolosus* (type locality Hunyani, Rhodesia) with 3 syntypes of *C. sudanensis* (type locality Imatong Mts., S Sudan). The two larger *sudanensis* workers have coarser and more abundant punctures, but the smaller one is almost identical with the *variolosus* syntype. The last is deep reddish brown in color; the *sudanensis* types are mahogany to piceous, and some workers from Gambari, Nigeria (B. Bolton) that I have determined as *sudanensis* are black.

### [31] *Cerapachys centurio* new species (Figs. 66-71)

Holotype worker: TL 5.7, HL (including frontal angle) 1.12, HW (immediately behind eyes) 0.83 (CI 74), greatest diameter of eye 0.25, scape L 0.81, WL 1.58, petiolar node L (dorsal view) 0.64, petiolar node W 0.57, postpetiolar node L 0.74, W 0.77 mm.

Paratype workers differ only slightly from holotype: TL 5.6-5.7, HL 1.05-1.10, HW 0.81-0.84 (CI 75-78), greatest

diameter of eye 0.24–0.25 (0.20–0.22 in series from S of Walikale), scape L 0.77–0.80, WL 1.46–1.55, petiolar node L 0.60–0.63, W 0.54–0.56, postpetiolar node L 0.65–0.72, W 0.73–0.77 mm.

Differs from the other African species of the genus in proportions, especially in having petiolar node distinctly longer than broad. Resembling *C. indicus* [56] in habitus, but with longer head, posterior margin transverse and straight behind in full-face view, sides only gently convex. Anterior face of clypeus lacking median tooth or carina (fig. 67). Foveolae of sculpture smaller than in *C. indicus* and more numerous, crowded, especially on petiole and postpetiole, where the interspaces are finely roughened and the whole surface subopaque. Small punctures on anterior gastric dorsum crowded, but interspaces shining, and posterior part of first segment smooth, with scattered small punctures. Standing hairs also decidedly more abundant than in *C. indicus*, especially on postpetiole and gaster (pilosity shows only poorly in fig. 70), where they are strongly inclined toward the rear. Pubescence not developed except for dense, short, reclinate hairs on coxae, lower metapleura, undersurfaces of petiole, front of petiolar node, and antennae.

Antennae with 12 distinct segments; pedicel slightly longer than broad; funicular segments II through IX broader than long; apical segment occupying about 2/5 of length of funiculus, and about 2.5 times as long as wide.

Other minor differences are that in *C. centurio*, the petiolar node is less narrowed in front than in *C. indicus*, and has a less sharply produced anterior margin; also, in *C. centurio* the subpetiolar process is compressed in front, and somewhat pointed as seen from the side, whereas in *C. indicus* the process is more lobiform and rounded in the same view.

Color dark brown with a slightly reddish tinge (darker than in *C. indicus*); without bluish iridescence; appendages lighter, more reddish.

Queen and male unknown.

Holotype (CAS—San Francisco) and 2 paratype workers from 15 miles S of Kamituga, Zaire, 700 m. 17 August 1957 (E. S. Ross and R. E. Leech). Also 3 paratype workers from 29 km S of Walikale, Zaire, 700 m (Ross and Leech). Paratypes in CAS—San Francisco, MCZ and BMNH—London. Further material in one or both of these series is available in CAS—San Francisco.

Further distinctions between *C. centurio* and the other African members of the genus are given in the key to the African—Middle East *Cerapachys* species.

[32] *Cerapachys wroughtoni* is a small, shining, sparsely punctulate species, bright ferruginous in color and, at least in the samples I have seen, lacking eyes (Forel Coll., Santschi Coll.). Forel described *C. roberti* as having minute eyes at the middle of the sides of the head, but in a specimen from the British Museum with the same label data as for

the *roberti* type (Estcourt, Natal, 1914, R. Wroughton), I could find no eyes at all. The hallmark of *wroughtoni*, the complete and deep, possibly even flexible, promesonotal suture, is present also in *roberti*, and I can see no way to separate these two forms. I have also seen specimens of *wroughtoni* (BMNH, MCZ) collected by R. E. Turner at Port St. John, Pondoland, Cape Province. The variety *rhodesiana* from Bulawayo is supposed to have a less well developed promesonotal suture than typical *wroughtoni*, but I believe it fits the latter well enough to be considered a synonym.

[33] Donisthorpe (1939) discussed the genus *Lioponera* and listed the species he considered to belong to it, remarking of the male: "The  $\delta\delta$  in the different species are superficially very like each other, and they do not possess sufficiently salient characters to separate them from those of the genus *Cerapachys* Smith." One wonders how, indeed, he was so sure that the two species he described as new in this same paper from males alone were not species of *Cerapachys*. Now that we know that *Cerapachys* and *Lioponera* are synonymous, the question of the African "*Lioponera*" males described by Santschi and by Donisthorpe (*noctambulus*, *decorsei*, *niger*, *similis*, *alfieri*, *cooperi*) becomes even more vexed. Some of these males could belong to species otherwise known under other names from workers, but it will probably be a long time until most of them are taken in association with the opposite sex.

Meanwhile, it seems overdue to point out that *parvus* and *bicolor* are obvious synonyms of *longitarsus*, and *australis* of Forel (1895, not 1900) is not different, either. It also seems so likely that Clark's *pygmaeus* is a worker of *longitarsus* that I have listed the synonymy; *longitarsus* occurs also at Darwin, N.T.; it lives in hollow twigs, and hence is likely to be carried oversea on floating branches, which may account for its wide distribution.

[34] *C. braytoni* was described in *Phyracaces*, but would have been placed in *Lioponera* by most authors. It is certainly rather close to *longitarsus*. This is another case illustrating the dangers of genera that are indistinctly separated.

The type of *braytoni* is from a point 29 miles SW of Mito Andei, Kenya, Jan. 1948, N. A. Weber No. 1954 (AMNH—New York). Holotype worker: TL 3.0, HL 0.62, HW 0.53, ML 0.08, scape L 0.31, greatest diameter of eye 0.23, WL 0.80, petiolar node L 0.23, W 0.37, postpetiolar node L 0.37, W 0.47 mm.

Bicolored: bright ferruginous; gaster (true IV abdominal and succeeding segments) deep piceous, nearly black. Shining; head, trunk and petiolar node indistinctly alutaceous, almost smooth, with scattered punctures. Postpetiole very finely and densely punctulate, subopaque; gaster densely punctulate and finely alutaceous, but shining. Pilosity fine, curved, oblique, moderate in length on head, and increasing in length up to about 0.20 mm caudad. Pubes-

cence fine, appressed to reclinate, sparse on head, trunk and petiole, very dense on postpetiole, moderately dense on antennae, legs, and gaster. A few longer erect hairs also on appendages.

Head in full-face view with convex sides and posterior margin, broadly rounded posterior angles. Eyes very large and convex, taking up nearly half of sides of head, situated near the anterior corners of the head.

Trunk without traces of dorsal sutures, weakly convex from side to side above, and from front to rear; declivity transversely marginate above. Node high, convex, weakly marginate above on the sides; seen from above, anterior corners prominent, but blunt; between them the anterior border is concave and feebly marginate; sides convex and slightly diverging behind; posterolateral corners obtuse, rounded, scarcely recognizable as angles; posterior border convex, immarginate. Postpetiole convex, rounded in front and rounding into convex sides.

[35] Males from Lebanon collected at light by K. Christensen in MCZ probably belong to *C. piochardi*.

[36] *Cerapachys lividus* new species  
(Figs. 46, 47, 50)

Holotype worker: TL 5.3, HL 1.00, HW 0.97 (CI 97), ML 0.19, WL 1.44, petiolar node L 0.51, petiolar node W 0.74, antennal scape L 0.56, greatest diameter of eye 0.30 mm (largest worker of type series).

Paratype workers: Measurements are of smallest paratype: TL 4.8, HL 0.94, HW 0.87 (CI 93), ML 0.15, WL 1.30, petiolar node L 0.48, petiolar node W 0.69, antennal scape L 0.51, greatest diameter of eye 0.28 mm.

Compound description: Form of head and body as in figs. 46 and 47. In larger specimens, head very nearly as broad as long; ignoring anterior projections over the mandibles, width is equal to or very slightly greater than length. In small specimens, head slightly narrower in relation to length. This is a thickest species with large, posteriorly placed eyes. A few of the larger specimens also have a weakly developed median ocellus, or ocellar pit, and in at least 2 specimens, minute, paired, posterior ocelli or pits are present.

Characters to be especially noted are the lack of a median tooth or tubercle on the clypeus; the obliquely raised, separated, frontal lobes and carinae; the large, smooth, impressed area mesad of each eye, serving as a demisrobe for the unusually large, thick 12-merous antennae; and, bordering each impressed area laterad, the distinct anteoocular groove connecting the circumocular (orbital) groove with the lateral carina of the cheek. The scapes reach to about the middle of the eyes; apical segment of antenna about  $3\times$  as long as penultimate segment, and slightly thicker. Palpi segmented 3,2, the two segments of the labial palpi both long.

Trunk boxlike, with sutures dorsum gently convex in both directions; pleura vertical, curving sharply into

dorsum above. Pronotum sharply marginate anteriorly, with a groove inside the margin; this groove, becoming wider and deeper ventrad, crosses the lower part of each side of the pronotum and continues horizontally across the middle of the side of the mesothorax as a deep mesopleural suture, then curves downward to form the suture between meso- and metapleuron. There is also a horizontal sulcus each, both above and below the meatus of the metapleurale gland. Propodeal declivity concave, bounded above and on the sides by a narrow, raised margin or carina. Propodeal spiracle situated down low, small, and nearly circular.

Petiole shown in figs. 47 and 50; note the concave dorsal surface and marginate anterodorsal edge, the latter very slightly convex in the middle, but otherwise straight. Sides of petiole steep, but not separated from dorsum by a margin. The longitudinal striation of the disc is distinctive. Postpetiole-gaster as shown in fig. 47. Sting stout. Pygidium with a smooth, shining, impressed disc, its lateral margins raised, bearing a row of sharp denticles.

Body surface smooth, with widely spaced, moderately coarse punctures, mostly piligerous, sparse on sides of trunk. Concave areas inside eyes and anterior clypeus impunctate; cheeks mesad of carinae, tibiae and tarsi, and sides of pygidium densely, finely, indistinctly punctulate, subopaque. Pilosity of fine, slightly curved hairs of moderate length, mostly decumbent to subdecumbent, fairly abundant (fig. 47), longest on gaster; shorter and dense on legs and antennae. Longer hairs more nearly erect in some specimens. Body black, with a rich, opalescent blue sheen; antennal funiculi, legs, and apex of gaster brown.

Apical tibial spurs narrowly pectinate, the posterior pair slightly larger than those of middle legs; tarsal claws slender and simple.

Queen and male unknown, unless some of the ocellate individuals act as queens.

Holotype (MCZ) and paratype (MCZ, BMNH, and elsewhere) from a series of 21 workers taken running in broken file over logs in wet forest near Périnet, on the rail line from Tananarive to Tamatave in Madagascar (Brown leg.). Some of the ants were carrying white pharate adults of a small *Pheidole* species, and they disappeared into cracks in a large rotten log that could not be opened with the tools available.

This species occupies a taxonomic position of special importance, because it links the old *Cerapachys* s.str. with *Phyracces* (by antennal form and shape of petiole) on the one hand, and with *Simopone* (by separate, merely obliquely raised frontal lobes, demisrobes, and very large eyes) on the other. The concave, medially striate disc of the petiolar node will serve to distinguish *C. lividus* from all congeners.

[37] *C. mayri* is a shiny black species of the "*Phyracces* habitus." Samples from several collections made in the wet forest of eastern Madagascar, including types of *mayri* and its variety *brachynodus*, seem to show that this species

varies fairly widely in size and proportions of petiolar node from one colony to the next. I judge that a single species is involved. At Périnet, Madagascar, I found this species raiding a *Phaidole* nest in the forest.

The specimen placed as "type" of *Parasyscia imerinensis* in the Forel Collection (MHN—Geneva) is actually a specimen of *C. mayri*, and the type queen of the true *imerinensis* could not be found in the collection.

[38] The *singularis* group consists of large and medium-sized red ants, some with a black or fuscous gaster, that possess a well-defined carina curving from the posterior corner of the head forward toward the compound eye, which it usually fails to reach (see inset figure in key, p. 27). This carina is a kind of anterior continuation of the sharp dorsolateral margins of the trunk and petiole, well developed in these species. In the small, black, forest species of the *tuneri* group from Queensland, the posterior corner of the head may bear a blunt ridge where the sides and the cervical surface of the head meet, but this does not form a sharp carina and does not curve toward the eye.

The *singularis* group is still poorly known, and some of the species coming out close together in the key may well be synonyms, particularly where one form is known only from the worker, and the other only from the queen, for example, *C. pictus* and *C. singularis*. I have synonymized the "subspecies" *rotula* under *singularis*, because they differ chiefly in whether the gaster is red or fuscous, and this character varies even in the *rotula* type series.

I have not been able to see the type of *Phyracaces emeryi* Viehmeyer, which may be a member of the *C. singularis* group, or else is one of the other large red species of arid-country *Cerapachys*. The trivial name *emeryi* is preoccupied in *Cerapachys*, but because the species is so likely to have been described under another name as well, I have not offered a *nomen novum* for it.

A worker syntype of *C. jovis* in MHN—Geneva is slender, with a rather strongly constricted trunk. Petiole subquadrate, sides nearly straight, very slightly converging caudad; posterior teeth short, obtuse, upturned. Trunk L from above (without declivity) 1.40; trunk W (maximum across propodeum) 0.84; petiole L without teeth 0.63, with teeth 0.66; petiole W 0.76 mm.

[39] Worker samples of *C. clarus* from National Park and elsewhere in southwestern Australia determined by Clark (possibly paratypes) and a winged queen paratype, also from National Park, compare so well with worker paratypes of *princeps* (type locality: Minnie Downs, NE corner of South Australia) that synonymy is indicated, and I am formalizing it at this time to avoid the proposal of a new name for Clark's *clarus*, preoccupied in *Cerapachys*. Samples of *C. princeps* are also in MCZ from Queensland: Brisbane (H. Hacker); and 5 km S of Marlborough, August 1972, short-grass pasture with *Eucalyptus* and *Melaleuca* trees,

ergatoid ♀ foraging in late-morning, bright sunlight (W. L. Brown).

*C. princeps* is distinguished among the large red species with ocellate workers by the long, acute teeth at the posterior corners of the petiolar node and by the straight, distinct anterior margin of the postpetiole.

[40] The lectotype (MCZ) of *C. rugulinodis* (by present selection) is one of two original cotypes and comes from Murat Bay, South Australia. Adherent moth scales indicate that it was taken at light. It probably belongs to one of the middle-sized red species formerly in *Phyracaces*. From the roughness of its petiolar and postpetiolar sculpture, one might suspect that it belongs with *C. clarki*, but the male of *clarki* is known and associated with workers, and it has the nodes merely finely reticulate and still shining; also, the subgenital plate (fig. 116) has a much different median lobe. In *C. rugulinodis*, the lobe is much longer and more slender, digitiform, with a bluntly rounded and slightly upcurved apical margin.

[41] *C. mullewani* is another species described from an isolated male (type locality: Mullewa, in central Western Australia), and probably belonging with workers of one of the large red species. *C. sjostedti* workers were collected at Mullewa by Wheeler in 1931, but some of the other red species are widespread in the arid Australian inland, and these possibly may occur also at this locality. The type of *mullewani* is presumably in the South Australian Museum at Adelaide.

[42] The names *Phyracaces fervidus*, *P. newmani*, and *P. fici* apply to slight variants of what I consider to be a single species. I have compared syntype series of *fervidus* from Cairns, Queensland, and Uralla, New South Wales (MCZ), directly with syntypes of *newmani* (Mundaring, SW Australia) and an additional series of topotypes of *newmani* determined by J. Clark, as well as a worker specimen of *fici* (USNM) from Trial Bay, N.S.W., the original locality, and probably a paratype. Variation, mostly between series but also to some extent within them, is seen in the depth and evenness of the mid-truncal constriction, convexity vs. near straightness of the cervical margin of the head, width of postpetiole, and the extent to which generally smooth, shining areas are replaced by very fine, sericeous, or even opaque, superficial sculpture.

This variation can be seen even within the *fervidus* type series. One pin of 3 "cotype" workers with a label from Uralla, N.S.W., probably mistaken by Wheeler for a Cairns label because only the similar-appearing bottom parts of the two labels on adjacent pins are easily seen beneath the point-mounts, shows well the differences in trunk and petiole form as compared with Cairns specimens, and displays slight differences also in sculpture. The *fici* specimen is most like the Uralla series, but it has the truncal constriction slightly deeper and more even. Of

the two sympatric *neumani* series, the "cotypes" are much more extensively smooth and shining, and only the front half of the head has the fine, shallow, reticulate sculpture in a relatively indistinct manifestation of this character. The topotypic series is darker red and has stronger (but still fine and weak) sculpture, not only over the dorsum of the head, but also over trunk, petiole, and postpetiole, to the extent that these parts are largely sericeous-subopaque at magnifications of 25 $\times$  and 50 $\times$ . The sculptural elements, particularly on the anterior face, may tend to be arranged in rows and thus in certain lights look like fine, indistinct striolation.

The type series of *P. scrutator* (MCZ), from Brisbane, Queensland, belongs to the *fervidus* complex, but the sculpture is still stronger and definitely opaque, extending over the head, trunk, petiole, and postpetiole. I think this species is only an extreme variant of *fervidus*, and it is provisionally placed as a synonym.

Then there is *P. leae*, described by Wheeler from a single worker from Townsville, Queensland, deposited in the South Australian Museum. Although I have not studied the type, I can find nothing in Wheeler's description or figure that will set this specimen apart from *fervidus* in the new, broad sense. Wheeler says that it "resembles *Ph. fervidus*, but is distinctly larger, even more shining and has a differently shaped thorax." Wheeler's measurements of ants were erratic and crude and usually give values significantly lower than I get (by measuring the separate tagmata axially, and then summing the lengths). Thus, Wheeler gives "Length 3.8-4.2 mm." for *fervidus*, "3.6-4 mm." for *scrutator*, and "5 mm." for *leae*. I measured the available samples of the complex discussed here at about 4.3 to 5.3 mm, and even if *leae* is really 6 mm long by my kind of measurement, that would not take it far out of the *fervidus* size range. As for the form of the "thorax", Wheeler's fig. 8 of *leae* shows a constriction much like that in some of the samples before me, while his fig. 9 of *fervidus* depicts a constriction somewhat less distinct than in the corresponding types, even those from Cairns. Thus it seems that differences in trunk shape, insofar as they really exist, are only those to be expected of a moderately variable species. Wheeler's words, "head and thorax very finely and superficially shagreened," also suggest that *leae* should be placed in the synonymy of *fervidus*.

Finally, I must add *P. dromus* and *P. flavescens* to this list of synonyms of *fervidus*. Paratypes of *dromus* and 2 additional topotypic workers (type locality is Patho in northern Victoria) are 4.4-4.8 long (TL), but are a trifle more slender and more shining than usual in *fervidus*; also, their petiolar teeth are a little smaller than usual. These differences are all in characters seen above to vary in *P. fervidus*, and I find them too slight to maintain *P. dromus* as a species apart.

Three paratype workers and an alate paratype queen of *P. flavescens* have very fine reticulation developed over

most dorsal body surfaces, especially the trunk, which is subopaque (more shining in ♀), but this is not as strong as in the *scrutator* types. The ♂ TL is about 4.2-4.4 mm, and for the ♀ about 5.5 mm. Clark said of *flavescens* that it is "near *P. neumani* Clark, from which it is distinguished by the color, sculpture and more slender form, as well as by the form of the node." By direct comparison of paratypes of *flavescens* and *neumani*, I can appreciate that *flavescens* is a little more slender and more opaquely sculptured, but I am unable to see anything more than the most trivial differences in color and petiolar node form. Type locality of *flavescens* is Eradu, W. Australia.

It is to be noted that some of the species here synonymized have apparently normal alate or dealate queens associated with the workers (*neumani*, *flavescens*), while in *dromus* the queen is ergatoid, although with mesonotum and scutellum indicated. I have assumed that ergatoids and winged queens both occur in *C. fervidus* s. lat., as in *C. clarki* and other species.

[43] In addition to the distinguishing characters given in the key, *C. incontentus* has the disc of the petiole, but not the postpetiole, rather densely covered with fine appressed, or at least reclinate, pubescence, best seen in oblique view. The name is a replacement for *inconspicuous* (Clark), preoccupied in *Cerapachys* by Emery, and is deliberately chosen with the first 5 letters the same, so that it will recall Clark's original name and will fall in about the same position in alphabetical listings.

[44] The two species *clarki* and *punctatissimus* are closely related forms that can be distinguished from other groups, in addition to the characters given in the key, by the peculiar sculpture of the discs of the petiole and postpetiole. These surfaces vary with the nest series and locality from weakly to strongly but very finely reticulate, and therefore range from subopaque to fairly strongly shining; but superimposed on this are numerous, rather densely crowded, moderately coarse, shallow punctures. Accompanying this sculpture is a variably dense, fine appressed pubescence, visible only in certain lights. The difference between the two species in the shape of the postpetiole is striking, and seems to be constant in the few series available.

[45] *C. ficosus* is widespread but rare in forested SE Australia. The MCZ has a series from Ferntree Gully, Victoria (J. J. McAreavey) and Macquarie Pass, New South Wales, 350 m (E. S. Ross and D. Q. Cavagnaro) in addition to the types from Bulli Pass, N.S.W. The Ferntree Gully workers (WL 1.2-1.3 mm) are smaller than the types (WL 1.8 mm) or the Macquarie Pass specimens (WL 1.7 mm).

[46] *C. ruficornis*, originally described from Mundaring and Armadale in SW Australia, has been found in the

lower end of Ravine des Casoars, W end of Kangaroo Island, South Australia, under a rock in tall mallee woodland (W. L. Brown), and at Wentworth Falls, 2800 feet, New South Wales (W. M. Wheeler). The Kangaroo Island specimens are considerably smaller (WL about 1.1–1.2 mm) than paratypes from Mundaring (WL 1.3–1.4 mm), and the Wentworth Falls sample is intermediate in body size. A specimen from Margaret River, SW Australia (W. M. Wheeler) is even larger than the types (WL 1.7 mm).

*C. ruficornis* is very similar to *C. adamus*, and for now, I am unable to separate these species satisfactorily from each other or from *C. turneri*. If we arbitrarily restrict *C. adamus* and *C. turneri* to Queensland material, we find that size is as variable in Queensland as it is in *ruficornis*. Samples placed as *adamus* (compared with the type by E. O. Wilson and by the author): Shipton's Flat, S of Cooktown (P. J. and P. F. Darlington) and near Kuranda, the type locality for *adamus* (W. M. Wheeler; W. L. Brown), do have the anterolateral corners of the postpetiole more sharply rounded, and this segment wider near the front and tapering slightly caudad, while in *ruficornis* the anterolateral corners are more gently rounded, and the widest part of the segment comes near midlength. However, the Wentworth Falls, N.S.W. *ruficornis* are intermediate in this character, as is also a worker referred to *adamus* from Tambourine Mt., S Queensland (A. M. Lea). Forel stressed larger size, larger eyes ("trois fois plus grands en proportion") and different head form for *adamus* as compared with *turneri*, but at least the difference in eye size is greatly exaggerated as shown by the types (MHN-Geneva) when compared. The *turneri* types do have the posterior teeth reduced more or less to rectangles, as also in a worker from Malanda in N Queensland (W. L. Brown) and one from Benarkin in S Queensland (P. J. and P. F. Darlington), but this could well be an allometric intraspecific difference. Only more material will clarify this situation, which I believe is best handled by leaving the species standing, even though they are not separated in the key. Still another nodal-form variant in this complex occurs in N Queensland; in this form, the petiole and postpetiole are both fairly long and are broadest near the front and tapered in the posterior half (Shipton's Flat, S of Cooktown; P. J. and P. F. Darlington). In view of the present uncertainties in the complex, I think description of this form as a new species would be premature.

[47] I have not seen the type of Clark's *C. aberrans*, from Kuranda, N Queensland, but I have 4 workers and a dealate queen from Crawford's Lookout above the Beatrix River, N Queensland (P. J. and P. F. Darlington) that agree with the *aberrans* description in the black body color and lack of all dorsal truncal margins, but differ in being smaller in size (♂ TL 4.4–5.1 mm, ♀ TL about 5 mm), with head longer than broad and with a gently concave posterior margin. The eyes are almost wholly with-

in the second quarter of the sides of the head (full-face view, starting at the anterolateral corners) and extend slightly beyond the second quarter, both front and rear. In *aberrans*, Clark describes and figures the eyes as being at the "middle of the sides," and he gives the head length and breadth as the same, and the posterior border as convex. The mandibles, antennae and legs in the Crawford's Lookout sample are light to medium brown, and not red in part, as Clark describes them; his length given is 6 mm, which may be a little low. *C. aberrans* is otherwise related most closely to *C. dumbletoni* of New Caledonia.

The tropical black Australian *Cerapachys* are all found in rain forest, usually in leaf litter.

[48] *C. binodis* seems to be a characteristic species of the Atherton Tableland region in N Queensland. In addition to the types, other specimens come from the type locality (Kuranda), collected by W. M. Wheeler. The Darlington took series on the Black Mt. Road, 1000–2000 feet, N of Kuranda; Lake Eacham; and W of Ravenshoe, about 3000 feet.

[49] I took a foraging worker of *C. brevis* on the ground on Anzac Hill at Alice Springs in C Australia, on 28 June 1951. The habitat was semidesert scrub with sparse mulga (*Acacia aneura*), and the ant was taken near midday. *C. brevis* was previously known only from SW Australia.

[50] The *C. suscitatus* type, originally described as a *Phyracces* from "Celebes, aus Kopal," is in MNK—Berlin. It is a slender species with the following approximate dimensions: HL 1.16, HW 0.94, max. W propodeum 0.76, petiole W 0.71, petiole disc L 0.61, postpetiole W 0.76, postpetiole L 0.85 mm.

Body black, almost completely covered with fine, even, dense but separated punctures. Petiole and postpetiole convex, with long hairs but without pubescence.

A depressed, vertical mesopleural strip is only sparsely punctate and therefore conspicuous. The petiole seen from above is subquadrate, with rounded sides, slightly wider behind, with subrectangular, not very prominent posterolateral angles.

*Phyracces hewitti* Donisthorpe (petiole W 0.73, petiole L 0.65 mm) is apparently the same species as *suscitatus*, and is certainly not a synonym of *P. hewitti* Wheeler, as Baroni Urbani has placed it. Although the homonymous species of Wheeler and Donisthorpe are both from the same type locality (Kuching, Sarawak), Baroni Urbani's (1971) statement that, "Beide Arten sind ziemlich sicher vom gleichen Material beschrieben," is contradicted by even a casual reading of the original descriptions, and of course also by the specimens themselves.

Specimens (MCZ) collected by R. H. Crozier in Malaya (Pahang: below The Gap) in hill forest probably belong to this species, but they have broader heads and trunks



than the Borneo-Celebes specimens, and their petiolar nodes are proportionately wider, with distinctly dentiform posterolateral angles: HL 1.29, HW 1.20, petiole L (including teeth) 0.62–0.63 mm. The sculpture is very similar. Other series in MCZ from the Cuernos Mts., near Dumaguete, Negros Oriental, Philippines (J. W. Chapman).

*C. suscitatus* is the analog of the Central African *C. nkomoensis*, but the two differ in details of body shape, and the punctuation of the African species is not so dense as in *C. suscitatus*.

[51] A small group of Indomalayan species related to *C. pubescens* and *C. hewitti* includes 2–3 probably undescribed species in MCZ and elsewhere, but the material available is inadequate for description. These black or dark brown species show interesting variation in the form of the petiole and postpetiole. In at least 2 of them, the petiolar node has inferior as well as superior posterolateral angles produced and sharply angular.

[52] Wilson (1959:47) synonymized *terricola* and its subspecies *tulagi* under *inconspicuus*, but this action may have been premature. Not only do the Solomons samples have finer punctures than *inconspicuus*, but their eyes are smaller (greatest diameter 0.17–0.19 mm) than in the *inconspicuus* collected by Wilson at the Busu River, near Lae, New Guinea (greatest diameter of eye about 0.23–0.24 mm). On the other hand, a very small worker from Maffin Bay, New Guinea (E. S. Ross; Wilson, *loc. cit.*) has exceptionally coarse, contiguous foveolae on the dorsum of the head, but the eyes are only 0.12 mm in greatest diameter. This small specimen, and some even smaller ("HW 0.49–0.50 mm"), were included by Wilson in *C. inconspicuus*, thus contradicting the statement in his key (1959:45, couplet 8) for *C. inconspicuus*, "Larger species, with head width (across and including eyes) less than 0.61 mm." Comparisons may of course involve allometry.

The confusion here envelops the species *flavaclavatus* and *dominulus*, both from N New Guinea; *C. flavaclavatus* (HW 0.46–0.54 mm *vide* Wilson) overlaps the smaller *C. inconspicuus* in head width. As a beginning at solving this problem, I propose that the sculpture rather than size be emphasized in the zone of sympatry, especially since size varies so much in this genus. In N New Guinea, *C. flavaclavatus* has widely separated pin-point punctures on the smooth and shining head, while *C. inconspicuus* has coarse and sometimes contiguous foveolae. In the Solomons, vicariant *inconspicuus* (or *flavaclavatus*) occurs in the form of *terricola*. Wilson implies that the Solomons populations represent the undisplaced *inconspicuus* existing away from the influence of *flavaclavatus*, and this may well be the correct interpretation, but the situation needs further study with more adequate material. The males should be studied, since the genitalia of *C. inconspicuus* are complex. Meanwhile, I have altered the key to reflect the above considerations.

The species *dominulus* was described from a single very small specimen (CAS—San Francisco) from Maffin Bay, New Guinea. Given the allometric differences often seen in the *C. dohertyi* group, this could well be a nanitic worker of *C. flavaclavatus* or some other species.

A series of workers from the Ayer Madidi slope of Mt. Klabat in N Celebes, from rotten wood in rain forest at 600 m (W. L. Brown) is very like the Busu River, New Guinea, *C. inconspicuus*, but is a little smaller, has the head a trifle shorter behind the eyes, and the corners more obtuse, the eyes are a little smaller and the petiolar node a bit shorter, and the color is darker reddish brown. The foveolate sculpture is very similar, and when we know more about *C. inconspicuus*, it may be possible to assign the Celebes population to this species.

[53] Wilson (1959:57) redescribed *C. dohertyi* and synonymized its var. *parvula* (type locality for both taxa is Pulau Laut, just off SE Kalimantan). I found the HW to be 0.93 mm in the holotype, not 0.95 mm; WL of holotype 1.42 mm. As Wilson noted, workers from Wai Lima, Lampong, S Sumatra (Karny) belong to this species; in fact, they are intermediate in most respects between Emery's types of *dohertyi* and var. *parvula*.

Type of *dohertyi* coarsely, contiguously punctate over head, trunk, both nodes; trunk with smooth shining areas with only scattered punctures on sides of promesonotum and on dorsum of mesonotum and propodeum. Eye diameter 0.30 mm. Type of var. *parvula*: HW 0.62, WL 0.92 mm. Sculpture more dilute, smooth; shining areas extensive, extending over most of sides and dorsum of trunk. Narrow smooth interspaces on vertex.

[54] The type of *Cerapachys conservatus* in MNK—Berlin is a member of the *dohertyi* group, WL 1.37 mm, with large eyes; petiolar node marginate anterodorsally. Head densely foveolate just mesad of eyes; upper vertex more sparsely punctate, with smooth, shining interspaces. Alitrunk with smaller spaced punctures. Petiole and postpetiole very densely and shallowly foveolate, the foveolae tending to be open behind; postpetiole with superimposed fine longitudinal striation, surface weakly shining to subopaque. Postpetiole slightly depressed and almost square — very slightly wider behind — with all corners rounded. Normally exposed terga of remaining gastric segments very densely punctate. It seems that the postpetiole and succeeding segments must have borne dense pubescence in life, before submersion in the copal resin. The shape and sculpture of the postpetiole and first gastric segment are unlike those of *C. dohertyi*.

[55] *C. bryanti* belongs to a small group of forms from Borneo, the Philippines, etc., of which it is the only species described so far. These species are marked by small size, flattened body (especially trunk), reddish color, and pre-

villingly smooth sculpture with small, spaced punctures. It is possible that at least some of these species also have larger workers with more convex trunk, as yet uncollected, because the related species *C. rufithorax* tends to show variation among the workers that joins these large and small forms, even in what appear to be single nest series.

[56] *Cerapachys indicus* new species

(Figs. 58–65, 72)

Holotype worker, from colony no. ICA-69: TL 4.7, HL (to anterolateral corners) 0.91, HW (without eyes) 0.77, ML 0.15, scape L 0.60, greatest diameter of eye 0.24, WL 1.35, L petiolar node (seen from above) 0.52, W petiolar node 0.49, L postpetiolar node 0.53, W postpetiolar node 0.57, L hind tibia 0.70, L hind metatarsus 0.59 mm.

Worker paratypes (7 measured), from type colony plus smaller-sized workers from Cardamon Hills, Geneva collection nos. 18 and 49: TL 4.3–5.5, HL 0.79–0.95, HW 0.63–0.87, ML 0.15–0.19, scape L 0.52–0.68, greatest diameter of eye 0.19–0.26, WL 1.17–1.45, L petiolar node 0.47–0.58, W petiolar node 0.41–0.55, L postpetiolar node 0.48–0.59, W postpetiolar node 0.50–0.63 mm.

Composite description: General form and many details of a paratype (HW 0.81, WL 1.44 mm) are shown in figs. 58 to 65. Descriptive remarks will be limited to those features not seen well in the figures and the variation in the material.

Head varying greatly in face (dorsal) view with only slight changes in position of the same specimen. Posterior outline of vertex in full-face view more or less convex, often with a shallow dip in the middle, but the posterior outline of the head as a whole is completed in full-face view at a lower (more ventral) level by its cervical border and posterolateral corners, and appears sharply truncate or weakly to distinctly concave when the focus is lowered slightly from the dorsal surface of the vertex. The posterolateral corners are rectangular to weakly acute in full-face view, and appear much more acute as the head is tilted forward (fig. 59). The median point or carina and the low, rounded lobe or apron of the clypeus, as well as the distinct denticulation of the mandibles, are shown well in fig. 62.

Petiolar node longer than broad, even if only slightly, in all workers seen up to petiolar node L 0.59 mm, which is the dividing line between worker and ergatoid in the Thirunelly series (type colony); nodes larger than this are ergatoid and are broader than long. The petiolar node has a sharp, raised, transverse anterodorsal margin and a lower, indistinct posterodorsal margin; the anterodorsal margin of the postpetiole is also sharply raised (fig. 63). The anterior face of the petiolar node is densely covered with decumbent, dorsally directed pubescence, as is the anterior postpetiolar face, though less densely. Propodeal declivity shallowly concave, minutely roughened, surrounded by a sharp, semicircular margin. Subpetiolar

process in side view rounded (type colony), bluntly pointed, or even bilobate (nos. 18, 49).

Two stray workers from near the type-colony site at Thirunelly have eyes smaller (diameter 0.16–0.18 mm) than in similarly large-sized workers of the type-colony series, but may belong to the same species. The two Cardamon Hills series are notably smaller in body size than the type-colony series. One of them (no. 18) has the foveae on the head smaller and less deep than in the other series, and the spaces between the foveae are wider, often wider than the foveae themselves on the upper vertex; but in these specimens, there is little if any reduction of the nodal and gastric sculpture. Faint lines marking the positions of promesonotal suture and metanotal groove are often present.

There is no apparent fine pubescence on the dorsal surfaces of nodes and gaster. The surface between foveae is prevalently smooth and shining, but with a microstructure that gives clean specimens a faint bluish iridescent sheen. Color mahogany; front of head, mandibles, apical antennal segment lighter, brownish red; gaster often darker than rest of body, approaching piceous.

Ergatoid (2 paratypes from type colony): TL 5.6–5.7, HL 0.97–1.02, HW 0.87–0.90, ML 0.15–0.19, scape L 0.67–0.68, greatest diameter of eye 0.25–0.27, WL 1.60 in both specimens, L petiolar node 0.60–0.61, W petiolar node 0.66–0.69, L postpetiolar node 0.71–0.75, W postpetiolar node 0.83–0.85 mm.

Like the workers of the same colony, but a little larger, with thicker body, especially nodes and gaster. Ocelli present on vertex, but small; the anterior ocellus may be very small.

Holotype (MCZ) and 12 paratypes from type colony (no. ICA-69) from the wooded ravine next to the temple at Thirunelly, Wynaad Taluk, about 900 m, Kerala State, India, 6 April 1969, A. B. Soans and W. L. Brown, Jr. This locality in the western Ghats still has trees shading a stream bed, and the soil was fairly moist at the time of collection. The colony was found under a stone, and stray workers were taken under other stones less than 100 m away. Other paratypes came from Winkler apparatus charged with leaf litter and forest floor debris, also from Kerala State, but farther south, in the Cardamon Hills: no. 49, 4 workers, Valara Falls, 46 km. SW of Munnar, 450+ m, 25 Nov. 1972; no. 18, 4 workers, between Pampanar and Peermade, 950 m., 9 Nov. 1972, team of Besuchet, Löbl, and Mussard from MHN–Geneva. Paratypes to be deposited in MCZ, MHN–Geneva, NM–Basel, and elsewhere.

In general habitus and its longitudinal petiolar node, *C. indicus* most closely resembles *C. centurio* [31] from central Africa, but differs from the latter in its shorter, more convex-sided head, and the deeper and more distinct, usually less crowded foveae of head and both nodes. Also, *C. indicus* has notably less abundant pilosity than *C. centurio*, and its color is a little lighter and more reddish. In

the oriental region, the most similar species is *C. dohertyi*, which has the petiolar node broader than long, the cephalic foveae more crowded than usual in *C. indicus*, and the foveae of the nodes smaller and less distinct.

[57] *Cerapachys luteoviger* new species

(Figs. 54–57, 90, 91, 93)

Holotype worker: TL 4.0, HL 0.82, HW 0.67 (CI 82), ML 0.10, scape L 0.53, greatest diameter of eye 0.20, WL 1.06, petiolar node L 0.37, W 0.49, postpetiole L 0.46, W 0.62 mm.

Paratype workers (9 from type colony): TL 3.9–4.0, HL 0.80–0.81, HW 0.65–0.68 (CI 81–84), ML 0.09–0.10, scape L 0.46–0.51, greatest diameter of eye 0.18–0.20, WL 1.01–1.04, petiolar node L 0.36–0.38, W 0.44–0.48, postpetiole L 0.42–0.46, W 0.57–0.60 mm.

Head, mandibles, and antennae shown in figs. 54, 55, 90, and 93. Posterior border straight to feebly convex when head is viewed full face. Median carina or tubercle of clypeus not well developed, not toothlike seen in full-face view (fig. 55). Trunk short and high, evenly convex above, parallel-sided, with transverse pronotal carina complete and forming subrectangular humeri as seen from above. Declivity of propodeum with carinate lateral margins, incomplete above in the middle.

Petiolar node distinctive in shape, as shown in figs. 56, 57, and 91; anterodorsal border concavely marginate (fig. 91). The body is smooth and shining, with spaced piligerous punctures as shown in the figures, except for petiole and base of first gastric tergum, which are more crowded with coarse punctures or foveolae (fig. 56), and postpetiole, which is densely covered with coarse and fine contiguous to subcontiguous piligerous punctures and very abundant longer and shorter decumbent hairs, consequently, its general surface only weakly shining. Posterior half of gaster smooth and shining, with only scattered, fine punctures. Propodeal declivity and anterior face of petiolar node smooth, shining, densely punctulate, and with a very fine appressed pubescence. Antennae and legs with moderate decumbent pubescence and some longer decumbent hairs (longer erect hairs also on scapes). Longer erect and suberect hairs of body moderately abundant, more abundant on postpetiole and gaster. Pygidium densely punctate, with a smooth, shining median strip; spinules in a single row on each side of apex.

Inner genual plate of hind coxae sharp and forming a crescentic margin, but not expanded as a lobe.

Color light ferruginous red, with posterior sides of trunk darker, more brownish. Apical segment of antenna light yellow, contrasting with the red of the rest of the body and appendages.

Queen (ergatoid): TL 4.5, HL 0.87, HW 0.73, (CI 84), ML 0.08, scape L 0.55, greatest diameter of eye 0.19, WL 1.21, petiolar node L 0.45, W 0.54, postpetiole L 0.52, W 0.78 mm.

Though this individual is very like the accompanying workers except in its notably larger size and bulkier body (especially the gaster), even Wilson, the original collector, noted that in life it seemed to be the “ergatoid queen.” I can find no distinct ocelli, though ocellar pits would be difficult to distinguish from the punctate sculpture. There is a distinct indentation on the mid-vertex, about where an anterior median ocellus would normally be found. The sculpture is perhaps a little more distinct than in the workers, and the petiolar summit is at least as sharply rounded as in the worker. The hairs of the pilosity are fine and tend to be more sharply erect than in the worker. Color as in worker.

Holotype (MCZ) taken from a small colony with the ergatoid queen from a piece of “*Passalus*-stage” rotten wood lying on the ground in forest at Gilimale, 16–20 km NE of Ratnapura, Sri Lanka (Ceylon), 18–21 July 1955, E. O. Wilson No. 1326. Wilson noted that the ants were very “nervous and active” in life. Paratypes in MCZ, BMNH—London, MHN—Geneva, and ANIC—Canberra.

This species is a member of the *dohertyi* group of the Indo-Melanesian area. Its closest relatives are 2–3 undescribed species from this general area, but it differs from all of these in details of head shape and sculpture, in the shape of the petiolar node apex, and in the color pattern; the yellow ovoidal apical segment of the antenna is characteristic and gives the ant its name.

[58] *Cerapachys kodecorum* new species

(Figs. 74–78)

Holotype worker: TL 4.3, HL 0.85, HW 0.76 (CI 89); HL includes frontal lobes, and HW is taken just behind eyes), ML 0.15, scape L 0.51, greatest diameter of eye 0.20, WL 1.13, petiolar node L 0.42, W 0.51, postpetiole L 0.52, W 0.63 mm.

Paratype workers (19 from type nest series) range downward slightly from the size of the holotype; smallest worker TL 3.7, HL 0.79, HW 0.70 (CI 89), ML 0.12, scape L 0.47, greatest diameter of eye 0.19, WL 1.00 mm.

General habitus, sculpture, and a number of particular characters are shown reasonably well in figs. 74–78, so I shall restrict my description to emphasizing the distinctive features and to those traits not well shown in the figures. The descriptive remarks apply to the whole type series.

Head broad, seen in full-face view posterior margin border straight to feebly convex, usually feebly concave in the middle, posterior border meeting convex sides at definite but obtuse angles. Eyes prominent, their middles situated slightly in front of midlength of head. Just anterior to each eye is a shallow but prominent indentation or scrobe running across the cranium to become subconfluent with its opposite mate at the midline, and together they form an arcuate sulcus (fig. 78) bounded in front by a sharp, irregular, semicircular carina that connects the

flanking cheek carinae (the carina does not show up well in fig. 78) and separates the anterodorsal part of the head, bearing frontal carinae and lobes and antennal insertions, from the main part of the vertex. Frontal lobes sharply obliquely raised, close together but not touching; extending posteriorly a short way as fine carinae, these also close together, subparallel, but separate. Descending anterior face of clypeus with an obscure median carina that appears as a minute tooth or tubercle in full-face view; translucent free apron of clypeus narrow, gently convex. Mandibles triangular, strongly curved ventrad, their basal margins curving into apical margins; the latter indistinctly denticulate (crenulate), smooth and shining, with spaced, coarse punctures. Anterior corners of head formed by prominent, subrectangular cheek carinae.

Antennae unusually strongly incrassate, especially across apex of scape (maximum width in holotype 0.23 mm; see fig. 78) and apical segment of funiculus (L 0.40, W 0.22 mm in holotype); 11 segments total in antennae, the 3 ring segments following the pedicel (III, IV and V from base of antenna) extremely short; all segments except scape and apical segment wider than long.

Trunk well shown in figs. 74-76; transverse anterior pronotal margin complete, sharp, raised; propodeal declivity also bounded by a distinct continuous margin. Petiole with a distinct anterodorsal margin. Subpetiolar process deep, narrowly rounded and laterally compressed, with a circular fovea in the middle.

Sculpture mostly well shown in the figures. Narrow interfoveolar interspaces of dorsum of head and trunk smooth and shining, also broad, smooth, and shining areas on dorsum of trunk in middle of mesonotum and propodeum, and on sides of trunk centered on mesopleura (figs. 74, 76). Propodeal declivity nearly smooth, shining.

Petiole and postpetiole densely and fairly coarsely foveolate, prevailing subopaque both above and below. Base of first gastric (IV abdominal) segment a little less coarsely, but still densely, foveolate at base, the foveolae becoming more spaced, and the intervals broad, smooth, and shining posteriorly. Pygidium densely punctate on sides, but smooth and shining on the midline. Legs finely and superficially punctulate, weakly shining. Clypeus mostly smooth; area just in front of arched carina of face nearly smooth, but crossed by sparse fine rugulae, behind antennal sockets.

Pilosity abundant, consisting of fine, obliquely erect hairs 0.10-0.20 mm long, sparse on legs and antennae, and shorter suberect to reclinate hairs, densest on petiole and postpetiole, but not forming a thick pubescence there. Legs with fairly abundant, fine, appressed pubescence, not very well shown in the figures.

Color dark reddish brown, legs lighter and more reddish.

Of the paratypes, one is abnormal, with head markedly flatter and broader than usual, with an asymmetrical impression in the left ventrolateral margin; this specimen

has only 7 funicular segments on the left side and 6 on the right. It is probably the result of damage to the growing larva or pupa.

Holotype (MCZ) and paratypes from a single nest (No. B-43) in a hollow, rotten stick embedded in leaf litter of mature lowland rain forest 20-25 km W of Batulitjin, SE Kalimantan (Borneo), at the end of June 1972 (W. L. Brown, Jr.). This locality is within the timber tract then being worked by the Korea Development Company (Kodeco), and the new species is named for my gracious Korean hosts, who made possible an exciting week of collecting in the forest.

Paratypes are deposited in MCZ, BMNH-London, ANIC-Canberra, and Cornell University Insect Collection, Ithaca, New York. This species is a rather typical *Cerapachys*, resembling members of the *dohertyi* group, but it may be distinguished from all known members of this group by means of its unusually thick antennae, with only 11 segments total and extremely short ring segments, and by the broad facial scrobal impressions to receive the retracted antennae in part (fig. 78). *C. kodecorum* is easily told from other 11-segmented Indo-Australian *Cerapachys* by its relatively large eyes and coarse, partly open sculpture.

No obvious queen, ergatoid or otherwise, was found in colony B-43, and the male remains unknown. The apparently pathological individual with reduced antennal segment numbers is interesting in pointing up how unstable the segment count, previously held to be a subgeneric character, can occasionally be even in a single nest series.

[59] *C. fossulatus* is bicolored like *C. aitkeni*, but is much larger and has a petiolar node longer than broad; the postpetiole is also just about as long as broad. The 11-merous antennae are of course diagnostic.

[60] *Cerapachys pruinosus* new species  
(Figs. 51, 52, 53)

Holotype worker: TL 4.4, HL (to external anterior insertions) 0.73, HW (excluding eyes) 0.69 (CI 92), ML (from insertions) 0.17, scape L 0.45, greatest diameter of eye 0.25, WL 1.14, L petiolar node 0.47, W petiolar node 0.46, L postpetiole 0.58, W postpetiole 0.59 mm.

Form of head and body as shown in figs. 51, 52, and 53, except that in dorsal view, the petiolar node is a little more nearly square, i.e. with more nearly straight sides, than as shown in fig. 53. The margin separating the dorsum from the sides of the petiolar node is fine and indistinct, and is best seen in an oblique view from above and to one side.

Mandibular teeth fine, irregular. Mesal genual plates of hind coxae developed as an obtuse-angled lobe on each side.

Dorsal surfaces of head, trunk, petiole, and gaster (except pygidium) very finely and densely punctate, the

punctures contiguous on front of head, and very nearly so elsewhere; interspaces or ridges between punctures shining, but so restricted that general surface is opaque to only feebly shining, punctures becoming slightly coarser and a little more widely spaced on lower sides of head, trunk, and gaster (which are therefore more shining), and also on apical gastric segments. Undersides of head and gaster have coarser (but still fine) punctures densely sown on a smooth, shining surface. Mandible, apical half of scapes, forelegs, and mesial surfaces of other legs and pygidium smooth and shining, with sparse punctures. Lateral surfaces of last two pairs of legs and all coxae finely punctate, moderately shining.

The most densely punctate parts of the body (dorsum of head and trunk, petiole, dorsum of gaster, bases of scapes, outer tibial surfaces of last two pairs of legs) covered with fine, short, dense, appressed whitish pubescence that lends a *Platythyrea*-like, pruinose appearance to much of the upper body surface. The legs, underside of head and especially of gaster with soft, appressed to decumbent pubescence over most sections normally exposed. Longer (but still modest), fine, standing hairs confined to anterior clypeus, mandibles, antennae (especially funiculi), a very few decumbent ones on the tibiae, and a few underneath and at apex of gaster. Color dark brown (piceous).

Holotype (MCZ) a unique from J. W. Chapman's Camp (about 1100 m elevation) in the Cuerneros Mountains, near Dumaguete, Negros Oriental, Philippines, "5/2/27," (Chapman).

The specimen lacks right anterior and middle legs, left hind leg, most or all of tarsi on the remaining middle and hind legs, and the apical half of the left funiculus, but tibial spurs are present on all the remaining legs. This species is very distinctive because of the extreme reduction of the standing pilosity and the pruinose sculpture-pubescent combination of the main body surfaces. It fits best in the group formerly called *Lioponera*, but it is larger than *longitarsus* or *luzuriagae* and much more densely sculptured than these.

The species described by Wheeler and Chapman as *Lioponera bakeri* must be similar to *pruinosis*, judging from the size given ("4 millimeters") and the very sketchy description and figure, but the type of *bakeri* was apparently lost in the destruction of the Bureau of Science in Manila during World War II. The description of *bakeri* reads in part: "Node of petiole as long as high, from above square, truncated in front, transversely rounded behind," which fits *pruinosis* passably well, as does "Densely punctured. . . Covered with fine recumbent pile." But "Hairs suberect, scattered, more abundant on scape and abdomen" apparently refers to a somewhat better developed standing pilosity than *pruinosis* has. Also, "Head coarsely rugose, finer on the remainder of the body," does not apply to *pruinosis*. The *bakeri* type came from Basilan Island, and we shall probably have to await further samples from there

before we find out what this species is really like. Incidentally, the *bakeri* scapes almost certainly do not reach "to the posterior occipital border;" their fig. 17 shows instead that the authors probably meant to write that the scape reached the posterior border of the eye.

[61] The variety *edentatus* is a straight synonym of *C. australis*. Forel apparently opened the mandibles of one of the 4 *edentata* syntypes now in his collection, and in doing so, broke off some teeth on or near the basal angle, which made the masticatory border appear edentate. Another worker from this series viewed in silhouette against a bright background proves to have the teeth usual for the species.

The younger name *edentatus* must prevail, however, because by the synonymy of *Lioponera* with *Cerapachys*, *C. australis* Forel is a junior homonym of *C. longitarsus* var. *australis* Forel, 1895.

I found a colony of *C. edentatus* with several hundred workers in a rotten log in a field near wet forest at Tambourine Mountain, S Queensland, and a single worker under a rock in the entrance gorge at Wilpena Pound, Flinders Ranges, S. Australia, in 1951. The latter represents a great extension of range.

The MCZ has material from other parts of Australia: Queensland: Brisbane (H. Tryon; H. Hacker). Between 5 and 15 miles N of Mareeba (P. F. Darlington). Northern Territory: Darwin (G. F. Hill). New South Wales: Kyogle (W. W. Froggatt); Mt. Wiagdon, 900 m (E. S. Ross and D. Q. Cavanagaro).

[62] The Melanesian species *C. papuanus*, *C. pusillus*, and *C. pawa* are poorly known and are only doubtfully distinct because of the sketchiness of their descriptions and a misunderstanding. Emery's original descriptions of *papuanus* and *pusillus* leave us in doubt as to whether the latter is just a smaller worker of the former, with allometric sculptural and node-proportion differences. A misunderstanding on the part of Mann (1919:277) led him to consider the postpetiole of *pusillus* "distinctly longer than broad," whereas Emery really described it as a trifle shorter than broad. The error was carried into Wilson's 1959 key.

It is possible that my stress in the key (couplet 78) on the shape of the anterior corners of the first gastric segment is also misleading, for it is based mainly on the only example of this complex that I have studied, a worker collected at Karema, Brown River, Papua, in lowland rain forest (E. O. Wilson, No. 573). Wilson already noted on the label that this sample was not completely typical of *C. papuanus*.

The *papuanus* complex needs careful study with the help of new material and the types. Types of *papuanus* and *pusillus* are in the Hungarian National Museum, Budapest (cotypes presumably in MCSN-Geneva), and the unique type of *C. pawa* must be in the USNM-Washington.

[63] I have known for a long time that *C. silvestrii* was the senior synonym of *C. sinensis*, *C. seini*, and *C. ierensis* after comparison of their types (Wilson and Taylor 1967: 33). Comparison of *silvestrii* digms with a syntype of *C. biroi* (MHN-Geneva) in 1963 and again in 1973 convinces me that these belong to one slightly variable species, even though the *biroi* type has the punctures of the head a little finer, and those on the trunk somewhat sparser, than in most *silvestrii* samples.

The type locality of *C. silvestrii* is Hilo, Hawaii; a cotype is in MCZ; *C. sinensis* type locality is Shanghai, China (cotype in MCZ); cotypes of *C. seini* and *C. ierensis* (MCZ) are from Rio Piedras, Puerto Rico, and St. Augustine, Trinidad, respectively, and additional material in MCZ comes from: Nepal: Amlekhganj, 500 m (E. I. Coher). India: Bengal, Baigachi (L. Weatherill). Okinawa: Iwa (F. G. Werner). Malaysia: Fraser's Hill, 4200 feet (E. S. Ross & D. Q. Cavagnaro). Hawaii: Oahu (R. H. van Zwaluwenburg).

Two indeterminate workers, HW 0.42 and 0.43 mm, taken by Ross and Cavagnaro in Australia, Northern Territory: Coomalie Creek on the Stuart Highway, 50 m elevation, have density of cephalic punctures intermediate between *biroi* and *edentatus*.

[64] ***Cerapachys besucheti* new species**  
(Figs. 79–83, 86)

Holotype worker: TL 4.4, HL 0.86, HW 0.79 (CI 92), ML 0.10, scape L 0.52, greatest diameter of eye 0.05, WL 1.17, petiolar node L 0.41, W 0.46, postpetiole L 0.41, W 0.52 mm.

Paratype workers (8) range downward in body size from that of holotype; where only one measurement is given for a structure, it is the smallest made: TL 4.1, HL 0.80, HW 0.71 (CI 88–92), ML 0.09–0.12, scape L 0.48, greatest diameter of eye 0.05–0.06, WL 1.05, petiolar node L 0.37, W 0.41, postpetiole L 0.40, W 0.47 mm.

Description based on all 9 workers from the type series: A robust member of the *fragosus* group, with 11 antennal segments and small but convex eyes with 20–30 distinct facets in the worker. Details of body form, sculpture, and pilosity are shown well in the figures, so I shall discuss only those characters that do not show well there and those that require emphasis.

Head broadest at just about its midlength, at the level of the compound eyes, tapering markedly in front of this, and only slightly behind. Posterior border of head transverse, shallowly concave in full-face view of head, at least in the middle. Anteromedian part of clypeus without a distinct median carinula or tooth. Mandibles triangular with acute apices and sharp, concave, edentate, masticatory borders; external borders straight at midlength; surfaces densely punctate, opaque, but apical third smooth and shining.

Petiole and postpetiole both broader than long, as seen

from above subtrapezoidal, wider behind, with the postero-lateral angles subtuberculate, especially in postpetiole. Anterior margin of petiolar node strongly convex, of postpetiole, transverse. Petiole and postpetiole reduced nearly to myrmicine proportions in relation to the enlarged first gastric segment, which dominates the gaster, even when, as in the specimen of fig. 83, the apical gastric segments are extended.

Head, trunk, and both nodes densely reticulate-punctate and prevalently opaque; gaster also densely and coarsely punctate, but less deeply so, shagreened, the spaces between punctures becoming appreciable only toward the rear of the first tergum, and even then only weakly shining, at most. The short but dense erect and suberect pilosity is supplemented by a still shorter, appressed to decumbent pubescence, best seen in fig. 82 between the larger pilosity hairs. Legs and antennae densely and finely punctulate, opaque or nearly so.

Color even dark reddish brown; light reddish brown in 2 specimens, probably still partly callow; legs scarcely lighter in color than body.

Queen (ergatoid): TL 4.7, HL 0.85, HW 0.77 (CI 91), ML 0.10, scape L 0.46, greatest diameter of eye 0.12, WL 1.22, petiolar node L 0.42, W 0.46, postpetiole L 0.48, W 0.56 mm. Workerlike, but larger and with relatively slightly more robust gaster; vertex with 3 distinct ocelli.

A second ergatoid is even larger: TL 5.1, HL 0.91, HW 0.86 (CI 95), ML 0.11, scape L 0.52, WL 1.36, petiolar node L 0.46, W 0.52, postpetiole L 0.52, W 0.64 mm. In this specimen, the anteromedian ocellus is well developed, but the paired posterior ocelli are indistinct, especially the one on the right side. Compound eyes with many facets, diameter 0.13 mm.

Holotype (MHN-Geneva) and paratypes from a small series taken mixed with other species of ants in a sample of soil and litter (run through a Winkler apparatus) from below Aliyar Dam in the Anaimalai Hills, 1150 m., Madras State, India, by the team of Besuchet, Löbl, and Mussard of MHN-Geneva, 18 November 1972. The species is named for Dr. Claude Besuchet, one of the collectors, a prominent specialist on pselaphid beetles and curator in charge of the famous Forel Collection of ants at the Geneva museum. In this latter capacity, Dr. Besuchet has played a key role in ant systematics through his cheerful and efficient accommodation of myrmecologists seeking aid with respect to the collection.

*C. besucheti* is clearly related to the 11-segmented species of the *fragosus* group—*C. fragosus* and *C. coecus* [65], but differs in being much larger, with larger, multifaceted eyes and broader, differently shaped petiolar and postpetiolar nodes; the head is also relatively broader and more tapered antierid. Paratypes in MHN-Geneva, MCZ, BMNH-London and ANIC-Canberra.

[65] The type of *Ooceraea fragosa* in the Roger Collection (MNHV-Berlin) is an ergatoid with well-developed com-

pound eyes and a single median ocellus. The specimen is very dirty, and it could not be cleaned by brush hairs because it is too small and fragile. Its head width is 0.46 mm. I compared with it 3 worker specimens collected in Winkler apparatus at Kantalai and Yakkala in Ceylon by the Besuchet-Löbl-Mussard team of MHN-Geneva; these specimens (HW 0.37–0.40 mm) are just about right in size, proportions, sculpture, and shape of petiolar and postpetiolar nodes to be the worker caste of *C. fragosus*. The apical antennal segment is a trifle thicker in the type than in the workers, and the antennal funiculi in the type as well as the workers appear to me to be 10-segmented, with the basalmost ring segment very small, possibly fused with the second, and snuggled into the basal funicular segment (pedicel) so that it is often hard to see. Eyes present as a pigmented spot and an indistinct facet, about as big as a neighboring puncture, in 2 of the 3 specimens. The petiolar and postpetiolar nodes in the workers are both slightly longer than broad as seen from above, and the anterior border of the petiolar node is rounded.

Seven workers also taken in Ceylon (Kandy, Kantalai) by the same (Geneva) team are larger and more robust (HW 0.55–0.60 mm) than *C. fragosus*, and have slightly coarser sculpture, and their petiolar and postpetiolar nodes are both slightly broader than long. I could find no remnants of eyes in these seven workers, which I take to be Mayr's "*Ooceraea coeca*" following his description. The funiculi also appear to be 10-merous, as in *C. fragosus*.

The *Syscia typhla* type in MNHU-Berlin has only 9 antennal segments, and the sculpture is shallower than in *C. fragosus*, with very fine opaque sculpture between the punctures on dorsa of head and trunk, instead of the fine shining rims separating the densely packed individual punctures of *fragosus* and *coeca*. A specimen of *C. typhla* in the Forel Collection (MHN-Geneva), apparently part of the original type series, has HL (including frontal carinae in this case) 0.60, HW 0.42, petiolar node L 0.26, W 0.25, postpetiolar node L 0.36, W (posterior) 0.36, L first gastric (IV true abdominal) segment 0.60 mm. Thus, *C. typhla* has the postpetiole more than half as long as the next (first gastric) segment, and is therefore transitional between "*Parasyxia*" and the more typical "*Syscia*" species, which have the postpetiole only  $\frac{1}{2}$  to  $\frac{1}{2}$  as long as the following segment.

The "*Syscia typhla*" of fig. 21 in Wilson and Taylor (1967) actually is *C. biroi* (= *C. silvestrii*); I had originally stated to the authors while they were preparing the paper my opinion that *silvestrii* and *typhla* were synonymous. When I found that the two names in fact applied to very different species, I communicated this to Wilson and Taylor, but in their manuscript the change was made only in the text, and was overlooked in the caption to their fig. 21.

*C. typhla* remains known only from the original Ceylonese collection.

[66] The *augustae* group consists of species with 11-merous antennae; eyes absent or reduced to a minute dot in the worker; sculpture consisting of coarse, crowded foveolae over head, trunk, and both nodes, and numerous large or small punctures on gastric dorsum. Queen with modestized, but convex and multifaceted compound eyes; in most of the queens seen, the pterothoracic sclerites are differentiated and blackened wing stumps are present, but ergatoid queens also occur.

From central Texas south to Panama, 14 different samples, ranging from 1 to 15 workers each (some with queens), have been examined, including syntypes of *C. augustae*, *C. toltecus* and *C. hondurians*. No two of these series are exactly alike, and taken all together, they show considerable variation in overall size, shape, especially of petiole and postpetiole, depth of color (yellowish ferruginous to deep brownish red), and above all in the size, density, and distribution of the foveolae and punctures of the integumental sculpture. Usually, series from one locality are much alike, even when from berlesates, but two series from Rancho del Cielo in the Sierra Guatemala of S Tamaulipas, Mexico, at about 1070 m in tall cloud forest with *Liquidambar* and *Podocarpus*, are quite different from each other in all of the characters just mentioned. One of these Rancho del Cielo series was taken by myself from a short, single-file column found moving on the ground beneath a log in July 1965, and the other came from a leaf litter berlesate taken by S. and J. Peck in July 1969. A few workers were taken under a rock in deep forest on Barro Colorado Island by myself in 1960, and most of the remaining samples came from forest litter berlesates from Mexico and intermediate Central American points. The Texas-Arizona samples are from much more arid localities.

While I do not believe that every sample represents a separate species, I cannot believe they all belong to one species. But I am unable to make a confident division of the species on the present evidence.

The males of this group are small, shiny, black or dark brown forms that are often taken at light in semidesert areas of Texas, New Mexico, and Arizona during July. These northern arid-land males have been placed with *augustae*, and a second species (*davisi*) was described by M. R. Smith, but none of them has yet been properly studied for genitalic characters. From the little we know of their habits, I assume that the workers of these species are subterranean, or at least cryptic, raiders of the nests of other ants. It should eventually be possible to collect living colonies and to rear males, and some male-worker associations may be needed to advance the hopeless-seeming taxonomy of this group. At the present time, it seems useless to try to key the species in the usual way.

[67] What I assume to be the males of *Sphinctomyrmex* in the MCZ and in the European ant collections have almost

all been taken at light or on the wing, away from the nest, so that few certain specific associations have been made with the worker-queen castes. I base the generic association, as did earlier authors, on the constrictions between the first 4 male gastric segments. There seems little doubt about this in the cases of the W African and Australian forms; an isolated male from the Nilgiri Hills in southern India (figs. 121, 129) corresponds to the worker-queen *S. furcatus* from the same general area [68] in size and color, and in having the principal gastric segments progressively shorter from front to rear, and separated by relatively weak constrictions. The *S. asper* male accompanied a queen and worker on the same pin.

These males show considerable specific differences in genitalia, and some of them have a well-defined, raised pygidium bounded by sharp margins, and peculiar bicornuate hypopygia (figs. 114, 120, 121, 127-129). Also interesting in *Sphinctomyrmex* is an apparent morphocline of male mandible shape, ranging from short-triangular (as in most male *Cerapachyini*) through short falcate to longer falcate (figs. 96-98). It seems reasonable to suppose that the males with falcate mandibles belong to those *Sphinctomyrmex* species with blind subdichthadiiform queens, by analogy with males having more or less similar mandibles in army-ant genera, where they are known or assumed to be used in grasping the queen during some phase of mating (Rettenmeyer, 1963:373, and contained references).

Future development of taxonomy and mating biology studies in *Sphinctomyrmex* probably depends on improved methods of collecting and rearing live colonies so as to obtain males in association with worker-queen castes.

[68] A. B. Soans and I found *Sphinctomyrmex furcatus* at Kottiyoor, in Wynaad Taluk, Kerala State, India in evergreen forest in the western Ghats at about 650 m elevation, 7 April 1969. The colony was in the humus and litter near a rotten log. Another colony was found at Thirunelly, about an hour's jeep ride away, under a stone in a shaded creek bottom. The ergatoid queen is scarcely different in size from the workers of the same nest, but she has somewhat larger compound eyes with fairly distinct facets, though they are still small and flat. The petiole is also shorter and wider than in the worker, and the integument more opaque, with finer sculpture and rather abundant, short pilosity-pubescent. Two of the queens were found in one colony. The groups of ants found were small, with less than 50 adults actually seen in each one, but they may have been foraging parties or fragments of larger colonies.

The Kerala specimens of *S. furcatus* are larger than *S. furcatus* syntypes in MCSN-Genoa and MCZ, but are otherwise similar. A syntype had petiolar node L 0.67, W 0.57 mm.

*S. taylori* with the ms. label name "*Cerapachys* (*Parasyscia*) *cocca* Forel" on a specimen in MCSN-Genoa from "Orissa, Indien" is apparently from the same series (MHN-Geneva)

that later became the *S. taylori* types. This is smaller (WL 1.27 mm) than *S. furcatus*, lighter (light ferruginous) in color, and has the petiolar node wider than long (L 0.44, W 0.49 mm). The truncal dorsum is also flatter than in *S. furcatus*, and the heavy, out-turned lateral margins of the propodeal declivity in *S. furcatus* are replaced in *S. taylori* by fine indistinct margins, widened into bumps only near their ventral ends. These differences could be allometric ones within a single variable species, but it seems best to recognize 2 species until more material is available.

A male (MCZ) from the Nilgiri Hills in southern India seems to fit the Kerala *S. furcatus* in size and in the similar proportions and constrictions of the main gastric segments. The hypopygium and genital capsule of this specimen are shown in figs. 121 and 129. This male has only 12 antennomeres total. It is prevailingly shining and dark reddish brown in color, with triangular mandibles.

[69] Through the courtesy of the late Dr. Felix Bryk, of the Naturhistoriska Riksmuseet in Stockholm, I was able to borrow the type of *Sphinctomyrmex stali*. It is a dealate queen bearing a pink label with "165" on it; another label reads, "Brasil/F. Sahlb[erg]." I was able to measure this specimen, and the results are offered with a few additional notes.

TL 5.7, HL 0.88, HW 0.76 (CI 86), scape L 0.52, WL 1.31, petiole L 0.43, gaster L (including postpetiole) 2.9 mm. When head is seen full face, median part of clypeus between frontal lobes concave, with a small median anterior tubercle, but no teeth springing anteriorly from the antennal sockets. Scape slightly curved and strongly incrassate toward apex. Petiolar node seen from above slightly more than  $\frac{2}{3}$  as long as broad; postpetiole about as long as broad; 3 succeeding segments distinctly broader than long.

Pygidium deeply concave and with raised margins set with acute denticuliform setae in a single row; concavity deepest caudad, and extreme apex emarginate. Wing stumps present. Body in general smooth and shining, with sparse, moderately coarse punctures, denser on front of head. Reddish ferruginous, appendages lighter.

Borgmeier (1957:104 ff.) described the worker of *S. stali* and figured it in detail. A worker received from him, collected by F. Plaumann at Nova Teutonia, Santa Catarina, Brasil, has HL 0.70, HW 0.56 mm, CI therefore 80. The punctuation is somewhat denser in the worker than in the type queen, and the color is dark reddish brown. Kempf (1972:241) also lists *S. stali* from the state of Guanabara in SE Brasil.

[70] With the type of *S. stali*, I also received from Dr. Bryk another winged queen of *Sphinctomyrmex* that he found bearing a Schönherr Collection label in the Naturhistoriska Riksmuseet, evidently deposited there in 1848 upon Schönherr's death. This specimen also bears the number "164" and another label, "S. Leone/Afzelius." Adam



Afzelius (1750-1838) was a sometime student of Linnaeus who collected in, or at least acquired material from, Sierra Leone. This specimen therefore must be nearly two centuries old.

The queen is similar to that of *S. stali* in size and proportions, but exact measurements were not made. Eyes much less convex than in *stali*, and placed a bit farther forward on the head. Median tubercle of clypeus longer, acute. Anterior borders of antennal sockets produced on each side of the median tubercle as a short, incurved tooth. Clypeal margin with a semicircular translucent lobe or lamella filling the space between the clypeus and the basal mandibular margins.

Pygidium concave, but not so deeply behind as in *stali*, apically gently emarginate, with denticuliform setae much more abundant and massed (not in one row), extending inward part way onto the concave surface.

Body sparsely punctate, shining, the punctures coarser on head. Color piceous, almost black; appendages and underside of gaster ferruginous. Venation of the forewing of the usual ponerine pattern, but weak apicad; Mf2 present, r-m wanting.

This specimen may well belong to one of the two African species described from the male sex by Santschi, and it does not seem wise to give it a name when we know so little about the African *Sphinctomyrmex*. Nevertheless, this example has considerable taxonomic significance because it establishes the presence on three separate continents of species in the genus with winged queens.

Still another *Sphinctomyrmex* is known from West Africa in the form of a series of workers found in the soil near the Lamto research station in central Ivory Coast by Dr. Jean Lévieux during his investigations of savanna ant ecology. Most of the available specimens are on loan to Dr. R. W. Taylor, who several years ago expressed an interest in describing them; so far no description has appeared. In my opinion, nothing much is lost in leaving this sample nameless until more material is available, and workers, queens, and males of the African *Sphinctomyrmex* have been properly associated.

A single worker of the Lévieux sample from Lamto (MCZ) is briefly described here in the interest of indicating at least what is present in West Africa.

*Sphinctomyrmex* sp., worker. TL 2.9, HL 0.56, HW 0.40, ML 0.06, WL 0.65 mm. Sides of head parallel, posterior margin concave. Eyeless. Frontal lobes vertical, very close together; no distinct median clypeal tubercle, no distinct teeth from the anterior edges of the antennal sockets. Antennae 12-merous. Trunk with a straight dorsal profile. Petiolar node appearing slightly elongate from side view, but about as broad as long seen from above. Postpetiole longer than succeeding segment, and just as deep seen from side view, but just about as long as succeeding segment, and narrower, with sides converging anteriorly, from dorsal view. The main gastric segments (postpetiole and true abdominals IV, V, VI) are about equal in length

as seen from dorsal view. Pygidium flattened apicad, but scarcely concave, and its free caudal margin rounded, with a narrow marginal band (about 2 denticles deep) of sharp slender denticles.

Shining, sparsely punctate, except dorsal surface of head, which has punctures larger and contiguous or subcontiguous except for a narrow smooth median strip. Color ferruginous yellow.

This species does not fit well the Afzelius queen, but there is no way of knowing whether it is the worker of one of the species described from males taken at light.

Very recently, Dr. W. H. Gotwald has shown me workers of an additional species of *Sphinctomyrmex* that he took during 1974 in Gabon, and which he intends to describe. The Gabonese species is decidedly larger than the Ivorian one described above, and is dark brown in color.

[71] The 3 yellow species of *Sphinctomyrmex* (*fulvidus*, *silaceus*, *brunnicornis*) with 12 antennal segments described by Clark from SW Australia seem to me to be the same as *S. imbecilis* Forel, also from this region.

The relationship of these forms has been obscured mainly by a lack of proper attention to the allometric variation of the workers and ergatoid queens. Large nest series usually include workers with heads only about 0.60 mm wide, or even less, ranging upwards to those with HW well over 0.80 mm, at which size they may already be entering the ergatoid range; there may be no sharp boundaries between the castes.

The smaller workers, HW about 0.60 mm, tend to have the head relatively narrower and more oblong, with only weakly convex sides and fairly abruptly rounded posterior angles, and the sculpture of the cephalic dorsum consists of a few moderately coarse, widely spaced punctures with wide, shining spaces between. At about HW 0.70 mm, the head is relatively wider and more convex-sided, and punctures are smaller and more abundant all over the dorsal surface, but are becoming particularly crowded in the anteromedial sector. At HW 0.80 mm and more, the head is relatively very wide, with rounded sides, and its dorsal surface is densely sown with small punctures (and the corresponding decumbent pubescence) throughout, to the point where the anterior quarter may be medially subopaque. Individuals at HW 0.90 mm or more may be classifiable as ergatoid queens, and traces of compound eyes can sometimes be found on the sides of the head, though not definitely pigmented in those I have seen in the MCZ.

Sometimes, on double- or triple-point mounts on a single pin, all the specimens will happen to be small workers, or all larger or medium ones, and it is easy to see how hasty examination of a few specimens in such cases might lead the viewer to think that he is dealing with different species. I will not discuss in detail Clark's terse remarks about species differences, because the cotypes and other series available either explain them in allometric terms,

or contradict them, and there is enough of Clark's material distributed in the more important collections so that the synonymy can easily be checked.

The "brown" funiculi Clark emphasized in describing *brunnicornis* do require a further word. Fuscous, even blackened, funiculi occur in some, but not all, workers of the *brunnicornis* type series (Collie, W. Australia), and also in another series from Swan River, W.A., determined as *brunnicornis* by Clark. Some of the latter also have one or more legs mutilated and blackened. I believe the blackened areas are healed or healing injuries due to mechanical or chemical damage inflicted by ants of other species defending their nests against the raids of the *Sphinctomyrmex*. At any rate, the blackened antennae are an irregularly appearing pathological trait, and not a reliable taxonomic character.

As Wheeler (1918:238) already remarked, the differences between *imbecilis* and *manni* are not very strong, and the material now available indicates that the squareness of the humeri and the distinctness of the dorsal margin of the propodeal declivity are variable characters in both eastern and western populations. I am unable to separate the two, and accept Wheeler's alternative view that they are variants of a single species, although I cannot accord them subspecies status. Furthermore, the differences between *imbecilis* and *froggatti* seem to me weak and variable, and it would not surprise me to see them synonymized by a future student with more material. Forel considered *imbecilis* as only a subspecies of *froggatti* when he first described the former.

## [72] *Sphinctomyrmex trux* new species

(Figs. 2, 101, 102, 105-113)

Holotype worker: TL 4.7, HL 0.87, HW 0.76 (CI 87), ML 0.12, scape L 0.50, WL 1.16, petiolar node L 0.38, W 0.48, postpetiole L 0.50, W 0.64 mm.

Paratype workers (21): TL 4.4-5.2, HL 0.84-0.94, HW 0.74-0.84 (CI 87-89), ML 0.12-0.15, scape L 0.47-0.54, WL 1.12-1.26, petiolar node L 0.40-0.44, W 0.44-0.50, postpetiole L 0.53-0.58, W 0.61-0.68 mm.

The figures show body form, pilosity, and some details of sculpture well enough; only features not, or poorly, shown or those needing emphasis will be described here.

Head with posterior border straight, extremely feebly concave in the middle as seen in full-face view, sides convex; eyes represented by pigmented dots at middle of sides of head, each without a distinct ommatidial facet. Frontal carinae with lobes sharply raised, subcontiguously converging and truncate behind; median carina of anterior slope of clypeus indistinct and forming only a low tubercle in full-face view. Anterior translucent apron of clypeus with a strongly convex border.

Mandibles triangular, with basal border rounding gradually into masticatory border, the latter finely crenulate on basal half, edentate on apical half; apex acute; external borders convex.

Labrum with a narrow median cleft in from the free margin; extensor surface with a transverse carina near midlength, in the middle forming a low, blunt transverse tubercle, also a small tubercle at either side of the labral shield, and a bluntly rounded tubercle or process at each side of an extension of the flexor face. Maxillary palpi 3-merous; first segment narrow; second segment long and broad, flattened, with a laterapical angle bearing 2 sensilla; apical segment small, its rounded apex bearing a single long sensillum. Labial palpi with a long, slender basal segment, subequal in length to the 2 shorter, broader distal segments taken together; apical and subapical sensilla 6-7.

Antennae with 12 distinct segments, all transverse except scape and apical segment, the last barely wider than preapical segment, and about 2½ times as long.

Sculpture and pilosity well shown in figs. 105-107, 109-111, and the sculpture fairly well for the petiolar disc in 112, but even here not all of the punctures near the center of the disc appear in the photograph; punctures of petiolar node decidedly smaller and more numerous than on truncl dorsum. Postpetiole and gastric terga all densely sown with punctures similar in size to those of the petiole, but much more numerous and crowded, many contiguous or subcontiguous, but all these surfaces nevertheless rather strongly shining. Pilosity of postpetiole and gaster, as can be seen from figs. 108, 109, 112, and 113, copious, suberect, with a conspicuous pubescence of appressed to decumbent, fine, short hairs. Antennae and legs punctulate, weakly shining, with long, fine decumbent pubescence (some longer suberect hairs on scapes); posterior faces of femora smooth and shining with scattered piligerous punctulae. Declivity of propodeum shining, microreticulate, with scattered piligerous punctulae.

Color medium brownish red; legs and antennae a little lighter and more yellowish.

Queen unknown.

Holotype (MCZ) and 21 paratypes (ANIC—Canberra, BMNH—London, MCZ, MHN—Geneva) taken near Ravenshoe, on the Atherton Tableland, N Queensland, Australia at about 3000 ft. (900+ meters) in April 1932 by P. J. Darlington, Jr.

This species has been compared directly with the types of all the related forms in the European museums, and it seems to be distinct in its particular combination of size, head shape, sculpture, and pilosity. There is, of course, the possibility that geographical or intrapopulation variation in some or all of these characters may be much greater than the available samples indicate, in which case some of these 12-segmented Australian *Sphinctomyrmex* may prove to be synonyms. I have seen males corresponding to at least 5 Australian *Sphinctomyrmex* species, however, and these are all quite distinct from one another. When we have reared colonies of this genus and get the males and queens in association with workers, the taxonomy will be more secure.

Meanwhile, the key to *Sphinctomyrmex* of the Indo-Australian region will help to distinguish this species.

### [73] *Sphinctomyrmex asper* new species

Holotype worker: TL 3.4, HL 0.67, HW 0.50 (CI 75), ML 0.06, scape L 0.34, WL 0.82, petiolar node L 0.29, W 0.30, postpetiole L 0.40, W 0.43 mm.

Habitus of small *S. steinheili*, or *S. duchsauyi*, and with the truncal dorsum almost perfectly flat and the color tawny, as in *S. duchsauyi*, but with antennae 12-merous and sculpture more dense and opaque.

Head oblong, with parallel, weakly convex sides and transverse (almost imperceptibly concave) posterior margin as seen in full-face view. Posterior corners rather sharply rounded. No eyes or remnants of eyes visible at magnification of  $\times 100$ . Frontal carinae short, close together, touching behind; anterior slope of clypeus between them with a minute tubercle or carina. Translucent apron of free clypeal margin much as in *S. steinheili*, narrowly rounded. Fused posterior frontal carinae continued posteriorly for a short way on anterior part of head as a fairly distinct carina.

Mandibles triangular, with basal border rounding into masticatory margin; the latter apparently edentate most of its length, but there may be a few minute denticles near the basal angle. Mandibular surfaces smooth with small, spaced punctures.

Trunk almost exactly twice as long as broad (excluding pronotal cervix, but including propodeal declivity), nearly parallel-sided, but slightly wider across the posterior half and very feebly constricted near midlength. Sutures obliterated; pronotal cervix separated from main part of pronotum by a shining, transverse, curved groove, but there is no distinct transverse pronotal margin. Propodeal declivity finely shagreened, subopaque, bounded by a weak margin on the sides and arching over the top.

Petiole node subquadratic, with nearly straight anterior and posterior margins and gently convex lateral ones. Postpetiole trapezoidal, with straight anterior and almost straight (very feebly convex), posteriorly diverging sides. First 3 (principal) gastric segments wider than postpetiole and just about equal to one another in width (0.53 mm) and length; slightly depressed. Last visible tergal segment (pygidium) narrower, tapering caudad, but with a subtruncate apex, perhaps even a trifle emarginate in the middle; marginal spinules in 1 or 2 rows.

The sculpture of *S. asper* is intermediate between those of *S. steinheili* and *S. caledonicus*, being more closed and opaque, i.e., with fewer and notably narrower smooth spaces between the foveolae than in *steinheili*, but with at least a few narrow, smooth, shining interspaces on middle of the sides of head and sides of pronotum, and even a few very narrow ones on the truncal dorsum, yielding a sparkle here and there if looked for carefully. *S. caledonicus* lacks these shining spaces, though the rims of the foveolae

themselves reflect some small weak points of light in the New Caledonia species.

In *S. asper* the petiole, postpetiole, and gastric dorsum are all densely punctate, and their surfaces are in general only moderately shining, the gaster more so than the nodes. Legs and scapes densely punctulate, opaque, femora weakly shining.

Pilosity short but abundant, tending to be appressed or decumbent over most of the body; a very few longer erect hairs, particularly near the apices of the gastric segments, may represent original standing pilosity, or may be the result of the brushing and ruffling needed to clean dirt particles from this old specimen. A few of these longer hairs on propodeum (perhaps ruffled erect), and a number at gastric apex, probably normally standing. Scapes and legs with appressed to decumbent pilosity.

Color uniform tawny yellow, the legs perhaps a bit lighter.

Queen (ergatoid): TL 3.9, HL 0.72, HW 0.54 (CI 75), ML 0.06, scape L 0.39, greatest diameter of compound eye 0.10, WL 0.94, petiolar node L 0.31, W 0.33, postpetiole L 0.40, W 0.48 mm.

Aside from its larger size, 3 distinct ocelli, and distinct, flat, subcircular compound eyes (with about 50, perhaps more, fine ommatidial facets), the ergatoid queen is little different from its worker. The sculpture is, if anything, still finer and more opaque, and the pilosity and color are much the same.

Male (postpetiole and gaster missing): HL 0.57, HW across and including eyes 0.64, ML 0.12, WL 1.17, forewing L 2.46 mm.

Translucent apron of clypeal margin sharply rounded, covering inner bases of closed mandibles, which are triangular; no space between mandibles and clypeus. Antennae 13-merous; pedicel about as broad as long, succeeding (second funicular) segment smaller, also about as broad as long; remaining segments all longer than broad; apical segment twice as long as penultimate segment.

Notauli distinct, forming a complete Y. Scutellum rounded and prominent. Propodeal declivity with strong lateral and dorsal margins, forming an angle in side view. Petiolar node rounded above, slightly broader than long.

Head contiguously and rather coarsely punctate and opaque. Mandibles shining, with scattered, fine punctures. Trunk densely punctate dorsally, with weakly shining interspaces. Scutellum, metanotum, and propodeum contiguously punctate, with a few rugulae, opaque; propodeal declivity striate-reticulate, subopaque; sides of pronotum and mesopleura sparsely punctate on a smooth and shining surface. Petiolar node indistinctly punctate and shagreened, subopaque. Pilosity short, appressed to suberect, pubescence-like. Color castaneous brown, mandibles and legs dull yellow; antennae light brown.

The holotype worker, ergatoid queen, and male were originally found in MCZ miscellany, pointed together on a single pin labeled as from Halifax, N Queensland, Aus-

tralia, June 1919, F. X. Williams. All are deposited in MCZ, and if additional material exists, I have not seen it.

The real relationship of *S. asper* will not be known until all of the Australian *Sphinctomyrmex* species are better represented in collections and associated with the proper males. *S. asper* is probably closest to the New Caledonian species, *S. caledonicus*, but, in addition to the characters cited in the key, *S. asper* is much lighter in color, is more slender, and has much straighter (less convex) sides of the postpetiole seen in dorsal view than does *S. caledonicus*; the latter species also has a distinct if fine transverse margin across the front of the pronotum.

[74] Wheeler (1918:228) has already shown that *S. steinheli* and *S. fallax* represent different castes of the same species. The subspecies *hedwigae* is just a slight variant of the variable *steinheli*, as far as I can see. Clark's species *hirsutus* and *fulvipes* are also just variants of *steinheli* in my opinion; syntypes of both have been compared with a syntype of *steinheli* and numerous samples from localities ranging from the Lofty Ranges of South Australia through Victoria, E New South Wales and Queensland, as far north as Mt. Lewis, near Mossman (P. F. Darlington). These samples range from yellowish ferruginous to dark reddish brown in color, but post-collection fading is probable in some of the lighter-colored samples. The density and coarseness of the punctures also vary moderately, as do the proportions of the head, petiolar node, and postpetiole seen in dorsal view.

The variety *cedaris* of *steinheli* is described as smaller than *steinheli* (about the size of *duchaussoyi*), and lighter, more yellowish in color. The ergatoid queen is said to have smaller eyes than *steinheli*, with only 8–9 facets. I have not studied type material of this species, but I suspect that it is a synonym either of *steinheli* or *duchaussoyi*. The types of *cedaris* come from Cedar Creek in N Queensland.

[75] An ergatoid queen syntype of *S. duchaussoyi* in the Emery Collection and a worker and ergatoid syntypes in the Forel Collection are smaller and much lighter (yellow) in color than adult *S. steinheli*, have relatively coarser, more-separated punctures on head and trunk, and are smooth and shining between the punctures. Both castes have slightly depressed bodies and 11-segmented antennae, and the ergatoid has 3 distinct ocelli and flat compound eyes about 0.08 mm in greatest diameter. Wheeler (1918:229) regarded this species as a variety of *S. steinheli*, but it seems to be distinct. In fact, *Eusphinctus hackeri*, described as new by Wheeler (1918) beginning on the same page (229), is the same as *duchaussoyi*. As he frequently did, Wheeler undermeasured the *hackeri* types rather badly, calling the worker "Length 1.5–1.7 mm". The syntype worker remaining in MCZ measures over 2.5 mm axially through the head and body, including mandibles. Wheeler apparently never saw authentic material of *duchaussoyi*. WL of the ergatoid runs about 0.70–0.81, while the WL of 2

workers is 0.60, 0.62 mm.

Distribution: Sydney, New South Wales, and Bribie Island near Brisbane, Queensland.

[76] *Simopone grandis* Santschi was described on specimens from Kunungu in what is now Zaire. Types are in MRAC –Tervuren and NM–Basel, and the MCZ has a worker specimen from Banga, Zaire, collected on a palm in swampy forest, 25 October 1926, by J. C. Bequaert (see figs. 87, 103, 104).

*S. grandis* has palpi segmented 6,4, and the head is of a relatively unspecialized *Cerapachys*-like form (fig. 87) rather than like that of most *Simopone*. The eyes are also placed farther back on the head, and are much more bulging than usual in *Simopone* species. *S. grandis* thus appears to be a rather primitive member of the *Simopone* stock – one that however, already (or convergently?) had lost an antennal segment to reach the 11-merous *Simopone* condition. In any case, *S. grandis* serves as a link between the *Cerapachys* and *Simopone* stocks. The laterally marginate petiole also suggests *Lioponera-Phyracces*.

*S. grandis* is easily recognizable by its large size and black body (Banga specimen: HL 1.97, HW across eyes 1.72, HW just behind eyes 1.64, WL 2.60, petiolar node L 1.20, W 1.05, greatest diameter of eye, faceted part, 0.60 mm), CI without eyes 93. Mandibles and antennae ferruginous, legs reddish brown. Ocelli present.

Petiole distinctly marginate on all 4 sides of disc; sides concave from top to bottom; anterolateral corners of postpetiole submarginate. Antennal segments 11; apical segment actually very slightly narrower than the preceding segment, and a little less than 3× as long. No distinct club. Maxillary palpi 6-segmented: basal segment short and thick; II longer, curved, broadened, blade-like; III, IV, V slender, apically clavate; apical segment fusiform. Labial palpi 4-segmented: basal segment short and thick; II broad and longer, flattened; III short and broad; IV short and digitiform. Middle legs without a distinct tibial spur, though perhaps one of the setae at tibial apex is the vestigial spur. Hind legs each with a single large, broadly pectinate spur; opposite this, the flexor surface of the slightly swollen metatarsus near its base is occupied by a prominent long-elliptical groove or pore, about ½ the length of the tarsomere, and filled with a white amorphous substance, apparently a dried secretion. Tarsal claws each with a median tooth. 3 ocelli present.

[77] *Simopone conciliatrix* new species  
(Figs. 11–13)

Holotype worker: TL 3.2, HL 0.63, HW 0.40, scape L 0.26; greatest diameter of compound eye 0.17, WL 0.78, petiolar node L 0.35, W 0.26, postpetiole L 0.34, W 0.34 mm; CI 63, petiolar node index 74.

Paratype workers, Ghana; 6 measured, including largest and smallest of 29 from type nest series: TL 2.4–3.4, HL

around the posterior edge of the sides of the head and meets its opposite number at the midventral groove of the head, thus encircling the true occiput.

Labrum with an emarginate free border. Palpi short, segmented 3, 2.

Trunk almost 3 times as long as wide, only very feebly constricted in the middle, with fine but distinct anterior pronotal margin; faint punctate sutural lines bounding the mesonotum in front and behind. Declivity of propodeum set off from dorsum and sides by a distinct, raised semi-circular margin. As seen from the side (fig. 11), dorsal outline of trunk nearly straight from mid-pronotum to declivity; only a very feeble impression centered on metanotal groove, and propodeal dorsum very slightly convex.

Petiole barrel- or loaf-shaped (figs. 11, 13), convex in both directions, as seen from above, with convex sides and widest near the posterior third; narrowed again slightly at posterior corners, which are rounded; anterodorsal border transversely marginate; seen in side view, a fine margin commences at the anterodorsal corner and runs back obliquely along the side to or near the posterior border below mid-height; this apparently represents the "Phyracces margin" of each side of the node. Subpetiolar process low, with a pointed anterior convexity bilaterally bearing "dimple" concavities, and a tapered posterior part, not very distinct in fig. 13. Postpetiole nearly or quite as broad as long, with convex sides and a little wider in the posterior part, but again narrowed at the posterior border, which is straight.

First gastric (IV true abdominal) segment a little broader than long (holotype: L 0.40, W 0.44 mm), widest in its posterior half, and then beginning to taper caudad; from this point, the 3 remaining visible segments tapering to apex with scarcely any intersegmental constriction. Pygidium with an impressed, nearly flat disc bordered laterally and caudad by a continuous U-shaped margin beset with 20 or more minute denticles; the stout sting issues from the true apex, which is beneath the denticulate margin.

Legs moderate in length, femora (especially fore femora) incrassate in the middle, tibiae moderately incrassate toward apices. Tarsal claws each with a small submedian tooth. Posterior tibiae each with a single broadly pectinate spur; posterior metatarsi without any obvious groove or pore on the basal flexor surface. Middle tibiae without spurs, unless one of the hairs at the apex represents a reduced spur.

Queen, dealate: TL 3.6, HL 0.62, HW 0.40, scape L 0.23, greatest diameter of compound eye 0.17, WL 0.93, petiolar node L 0.37, W 0.25, postpetiole L 0.38, W 0.35 mm; CI 65, petiolar node index 68. Ocelli well developed. Pterothorax and blackened wing structures well developed, but the trunk still rather flat, only weakly convex above, broadest across the middle.

First gastric (IV true abdominal) segment about as long as broad, or perhaps a trifle longer than broad. Otherwise as in worker.

Male unknown.

Holotype worker (BMNH) taken from a nidotype series of 103 workers (BMNH, MCZ) and two dealate queens (BMNH) with larvae from a nest in a hollow twig of cacao still on the tree at Tafo (New Tafo, "Akim"), Ghana, on 27 November 1970, by Barry Bolton. The nest was about 2 meters above the ground in moderate shade.

In addition, two workers from Yangambi, Réserve Intégrale R. "Luco," in what is now Zaïre, 6 October 1949, A. Raignier and J. van Boven, no. C-1265, are in MCZ.

This species is named *Simopone conciliatrix* because it shows a mixture of characters of *Lioponera* (= *Phyracces*), *Simopone* and *Cerapachys*, thus tying these genera together. In general habitus (elongate head and petiole, large eyes), *conciliatrix* is a *Simopone*. The frontal carinae are fairly close together, but parallel and separate caudad; they are intermediate between the condition seen in *Simopone* on one hand and *Lioponera-Cerapachys* on the other. The lack of ocelli in the worker and the 12-merous antennae are shared by *conciliatrix* with the majority of (but by no means all) *Cerapachys-Lioponera*. Toothed tarsal claws are a character of *Simopone*, but one also found in a few *Cerapachys*, including the type species of that genus. The petiole, with its weak lateral margins and barrel-like shape, combines traits of *Simopone*, *Lioponera*, and *Cerapachys s.str.*

*S. conciliatrix* is not closely related to *S. grandis*, another species linking *Simopone* and *Cerapachys*, and the greatly elongate head will separate *conciliatrix* from all 12-segmented *Cerapachys*. The lack of spurs on the tibiae of the middle legs is considered here as definitive in placing the species in *Simopone*.

[78] I examined the unique worker type of *Simopone schoutedeni* in the Musée Royale du Afrique Central in Tervuren, Belgium, during late April 1973, and on the same day I was given a specimen of the species from Yangambi, Zaïre (A. Raignier and J. van Boven) by Dr. van Boven, who has since sent me two more workers from the Yangambi series. The type as found was very dirty and partly covered with glue, much of which I was able to clean off. The outline was somewhat changed in the process, and the sculpture became clearer and more shining. The head is 0.97 mm long; HW 0.67 behind eyes, including eyes 0.68 mm. WL 1.24 mm. Petiole L 0.52, W 0.48 mm, disc very slightly narrowed in front, and margined both front and rear, appearing almost square. As seen from above, sides of trunk nearly parallel and with only a faint suggestion of constriction at midlength; both promesonotal and metanotal sutures indicated and more or less punctate, but not deeply impressed.

Head coarsely punctate; space between eyes and frontal carinae forward also finely longitudinally reticulate-striate, subsericeous. Coarse punctures also spaced on the shining truncal dorsum, which is basically smooth, but shows feeble, fine shagreening in some lights. Petiole and post-

petiole more densely and finely punctate, and gaster still more finely so, but still shining. Pilosity reclinate, grading into shorter, mostly reclinate, white pubescence, more dense on nodes and gaster. Eyes with short erect hairs. Black, clypeus and femora brown; antennae, tibiae, and tarsi and mandibles yellowish.

The Yangambi specimens are smaller; one worker had WL 1.10, petiole disc L 0.44, W 0.47 mm (thus slightly wider than long), and the petiolar-postpetiolar punctures are a bit finer. The type of *Simopone wilburi* Weber was compared with Yangambi specimens in May 1973, and it proved to be more like the *schoutedeni* type, but even larger: WL 1.45, petiole disc L 0.57, W 0.52 mm. Weber's stated differentiation of *wilburi* from *schoutedeni* seems to have been based on Santschi's description and his rather sketchy figure, both of which evidently suffered from the dirtiness of the specimen. I judge the respective types to be conspecific.

A worker agreeing well with the description of *S. conradi* was taken by W. H. Gotwald on the Forêt du Plateau, near Lamto Research Station in C Ivory Coast.

[79] Wheeler's *C. williamsi*, described from the Galapagos, is just *C. striatus* with darker legs than usual. Even so, the

tibiae of the types do have limited pale areas on the extensor surfaces, and are not "black" as Wheeler described them. This species, like other *Cylindromyrmex*, shows appreciable allometric variation, and size varies considerably, even in single nest series. When workers of the same size are compared, the *williamsi* types and mainland samples are very similar in the shape of the head, petiole, and tibiae. The variety *tibialis* is reasonably clearly another synonym of *striatus* from the Galapagos, with more normal light tibiae, as in a series from Fernandina in the Galapagos collected by Robert Silberglied.

In addition to the *williamsi* types, the MCZ has samples of *striatus* from Ecuador: Hac de Tengel (W. von Hagen). Guayaquil (C. T. Brues; F. X. Williams). Babahoyo (H. Hanson). Galapagos, Isla Fernandina, about 3 km inland from coast on N side, about 45° m, under bark (R. Silberglied). Peru: Chiclayo (W. Weyrauch).

[80] A dealate queen agreeing well with the (headless) type of *C. boliviæ*, except that it has the concave sides of pronotum distinctly longitudinally striate, comes from Rancho Grande, Aragua Prov., Venezuela, about 1100 m, "on a low leaf" (N. A. Weber, no. 4791). This locality is wet mountain forest.

## REFERENCES CITED

- André, Ern.  
1890. Matériaux pour servir à la faune myrmécologique de Sierra-Leone (Afrique occidentale). Rev. Entomol., Caen 9:311-328.  
1892. Matériaux myrmécologiques. Rev. Entomol., Caen 11:45-56.  
1909. Description d'un genre nouveau et de deux espèces nouvelles de Fourmis d'Australie. Rev. Entomol., Caen 28:205-208.
- Arnold, G.  
1915. A monograph of the Formicidae of South Africa (Ponerinae; Dorylinae). Ann. S. Afr. Mus. 14:1-159, pl. 1.  
1926. A monograph of the Formicidae of South Africa. Appendix. Ann. S. Afr. Mus. 23:191-295.  
1954. New Formicidae from Kenya and Uganda. Ann. Mus. Congo, Tervuren, Zool. (quarto) 1: 291-295.  
1955. New species of African Hymenoptera. No. 11. Occas. Pap. Natl. Mus. S. Rhodesia 20:733-762.  
1960. Aculeate Hymenoptera from the Drakensberg Mountains, Natal. Ann. Natal Mus. 15:79-87.
- Ashmead, W.  
1906. Classification of the foraging and driver ants, or family Dorylinae, with a description of the genus *Ctenopyga* Ashm. Proc. Entomol. Soc. Wash. 8:21-31.
- Bernard, F.  
1952. La réserve naturelle intégrale du Mt. Nimba. XI. Hyménoptères Formicidae. Mém. Inst. Fr. Afr. Noire 19:165-270.
- Borgmeier, T.  
1955. Die Wanderameisen der neotropischen Region. Studia Entomol. (n.s.) 3:1-720, pl. 1-87.  
1957. Myrmecologische Studien. I. An. Acad. Brasil. Cienc. 29:103-128.
- Brown, W. L., Jr.  
1952. Contributions toward a reclassification of the Formicidae. I. Tribe Platytithreini. Brev. Mus. Comp. Zool. Harv. 6:1-6.  
1954. Remarks on the internal phylogeny and subfamily classification of the family Formicidae. Insectes Sociaux 1:21-31.  
1955. The ant *Cerapachys rufithorax* and its synonyms. Psyche 62:52.  
1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). Bul. Mus. Comp. Zool. Harv. 118:173-362.  
1960. Contributions toward a reclassification of the Formicidae. III. Tribe Amblyoponini (Hymenoptera). Bul. Mus. Comp. Zool. Harv. 122:143-230.  
1963. Characters and synonymies among the genera

- of ants. Part III. Some members of the tribe Ponerini. *Brev. Mus. Comp. Zool. Harv.* 190:1-10.
1965. Contributions toward a reclassification of the Formicidae. IV. Tribe Typhlomymecini (Hymenoptera). *Psyche* 72:65-78.
1973. A comparison of the hylaeian and Congo-West African rain forest and faunas. In *Tropical forest ecosystems in Africa and South America: A comparative review* (B. J. Meggers, E. S. Ayensu, and W. D. Duckworth, eds.), pp. 161-185. Smithsonian. Inst. Press, Wash., D. C.
- Brown, W. L., Jr., and Nutting, W. L.  
1950. Wing venation and the phylogeny of the Formicidae. *Trans. Amer. Entomol. Soc.* 75:113-132.
- Brown, W. L., Jr., and Taylor, R. W.  
1970. Superfamily Formicoidea. In *The insects of Australia*. Univ. Melb. Press, Melbourne. xiii + 1029 pp.; cf. pp. 951-959.
- Bruch, C.  
1924. Una nueva ponerina, *Acanthostichus ramos-mexiae* n. sp. *Physis* 7:260-261.  
1925. Macho, larva y ninfa de *Acanthostichus ramos-mexiae* Bruch. *Physis* 8:110-116.  
1934. La hembra dictadiiforme de *Acanthostichus laticornis* For. v. obscuridens Sants. (Hymenoptera Formicidae). *Rev. Soc. Entomol. Argentina* 6:3-8, pl. 1-2.
- Cameron, P.  
1891. In E. Whymper. *Travels amongst the great Andes of the equator*. Suppl. appendix, pp. 89-95.
- Charnley, H. W., Jr.  
1973. The value of the propodeal orifice and the phallic capsule in vespid taxonomy (Hymenoptera, Vespidae). *Bul. Buffalo Soc. Natur. Sci.* 26:i-iii + 1-79.
- Clark, J.  
1923. Australian Formicidae. *J. R. Soc. W. Australia* 9:72-89.  
1924. Australian Formicidae. *J. R. Soc. W. Australia* 10:75-89, pl. 6, 7.  
1926. Australian Formicidae. *J. R. Soc. W. Australia* 12:43-51, pl. 6.  
1929. Results of a collecting trip to the Cann River, East Gippsland. *Vict. Naturalist* 46:115-123.  
1930. New Formicidae, with notes on some little-known species. *Proc. R. Soc. Vict., Melbourne*, (n.s.) 43:2-25.  
1934a. New Australian ants. *Mem. Nat. Mus. Vict., Melbourne*, 8:21-47, pl. 2, 3.  
1934b. Ants from the Otway Ranges. *Mem. Nat. Mus. Vict., Melbourne*, 8:48-73, pl. 4.  
1938. The Sir Joseph Banks Islands. Reports of the McCoy Society for Field Investigation and Research. Part I. Formicidae. *Proc. R. Soc. Vict.* (n.s.) 50:356-382.
1941. Australian Formicidae. Notes and new species. *Mem. Nat. Mus. Vict., Melbourne*, 12:71-94, pl. 13.
- Consani, M.  
1951. Formiche dell'Africa Orientale. I. *Boll. Ist. Entomol. Univ. Bologna* 18:167-172.
- Crawley, W. C.  
1915. Ants from north and central Australia, collected by G. F. Hill. Part I. *Ann. Mag. Natur. Hist.* (8)15:130-136.  
1922. New ants from Australia. *Ann. Mag. Natur. Hist.* (9)9:427-448.  
1923. Myrmecological notes. *Entomol. Rec. J. Var.* 35:29-32.  
1924. Ants from Sumatra, with biological notes by Edward Jacobson. *Ann. Mag. Natur. Hist.* (9)13:380-409.  
1925. New ants from Australia.-II. *Ann. Mag. Natur. Hist.* (9)16:577-598.  
1926- A revision of some old types of Formicidae. (1925). *Trans. Entomol. Soc. London* 373-393.
- Donisthorpe, H.  
1931. Descriptions of some new species of ants. *Ann. Mag. Natur. Hist.* (10)8:494-501.  
1932. On the identity of Smith's types of Formicidae (Hymenoptera) collected by Alfred Russell Wallace in the Malay Archipelago with descriptions of two new species. *Ann. Mag. Natur. Hist.* (10)10:441-476.  
1938. New species of ants and a new subgenus of *Dolichoderus* from various localities. *Ann. Mag. Natur. Hist.* (11)2:498-504.  
1939. The genus *Lioponera* Mayr (Formicidae, Cera-pachyinae), with descriptions of two new species and an ergatandromorph. *Ann. Mag. Natur. Hist.* (11)3:252-257.
- 1941a. Descriptions of new species of ants from New Guinea. *Ann. Mag. Natur. Hist.* (11)7:129-144.  
1941b. Descriptions of new ants (Hym., Formicidae) from various localities. *Ann. Mag. Natur. Hist.* (11)8:199-210.  
1947- Ants from New Guinea, including new species (1946) and a new genus. *Ann. Mag. Natur. Hist.* (11) 13:577-595.  
1948- A third installment of the Ross Collection of ants (1947) from New Guinea. *Ann. Mag. Natur. Hist.* (11)14:589-604.  
1949- A fifth installment of the Ross Collection of ants (1948) from New Guinea. *Ann. Mag. Natur. Hist.* (12) 1:487-506.
- Emery, C.  
1882. *Parasyscia*. In *Species des Hyménoptères d'Europe & d'Algérie*, (André, ed.) 2:235-236.  
1886. Alcune formiche africane. *Bul. Soc. Entomol. Ital.* 18:355-366, pl. 17.

1887. Catalogo delle formiche esistenti nelle collezioni del Museo Civico di Genova. Parte terza. Formiche della regione Indo-Malese e dell'Australia. Continuazione e fine. Ann. Mus. Civ. Stor. Natur. Genova. (25):427-473, pl. 1, 2.
1889. Viaggio di Leonardo Fea in Birmania e regioni vicini. XX. Formiche di Birmania e del Tenasserim raccolte da Leonardo Fea (1885-87). Ann. Mus. Civ. Stor. Natur. Genova (27):485-520, pl. 10, 11.
1890. Voyage de M. E. Simon au Venezuela. Formicides. Ann. Soc. Entomol. France 39:55-76.
- 1893a. Formicides de l'Archipel Malais. Rev. Suisse Zool. 1:187-229, pl. 8.
- 1893b. Intorno ad alcune Formiche della Collezione Spinola. Bol. Mus. Zool. Univ. Torino 8(163): 1-3.
- 1894a. Studi sulle formiche della fauna neotropica. VI-XVI. Bul. Soc. Entomol. Ital. 26:137-242.
- 1894b. Formiche di Birmania del Tenasserim e dei Monti Carin raccolte da L. Fea. Ann. Mus. Civ. Stor. Natur. Genova (2a)14:450-483.
- 1895a. Die Gattung *Dorylus* Fab. und die systematische Eintheilung der Formiciden. Zool. Jahrb. Syst. 8:685-778.
- 1895b. Voyage de M. E. Simon dans l'Afrique australe (janvier-avril 1893). Formicides. Ann. Soc. Entomol. France 63:15-56, pl. 2.
1897. Formicidarum species novae vel minus cognitae in collectione Musaei nationalis hungarici, quas in Nova-Guinea, colonia germanica, collegit L. Biró. Természetr. Fü. 20:571-599, pl. 14, 15.
- 1899a. Intorno alle larve di alcune formiche. Mem. Accad. Sci. Ist. Bologna (5)8:3-10, 2 pl.
- 1899b. Fourmis d'Afrique. Ann. Soc. Entomol. Belg. 43:459-504.
- 1900- Formiche di Madagascar raccolte dal Sig. A. (1899). Mocquers nei pressi della Baia Antongil (1897-1898). Bul. Soc. Entomol. Ital. 31:263-290.
- 1901a- Formiche raccolte da Elio Modigliani in Sumatra, Engano e Mentawai. Ann. Mus. Civ. Stor. Natur. Genova (2a)20:659-722.
- 1901b. Notes sur les sous-familles des dorylines et ponerines. Ann. Soc. Entomol. Belg. 45:32-54.
1902. Note mirmecologiche. Rend. R. Accad. Sci. Ist. Bologna, (n.s.) 6:22-34.
1911. Subfamille Ponerinae. Genera Insectorum, fasc. 118, pp. 1-125, pl. 1-3.
1923. Einige exotische Ameisen des Deutschen Entomologischen Institutes. Entomol. Mitt. 12:60-62.
- Forel, A.
1886. Espèces nouvelles de fourmis américaines. Ann. Soc. Entomol. Belg., (c.r.) 30:38-49.
1891. Les formicides. In Grandidier, A. Hist. phys. nat. polit. Madagascar 20(2):1-243, pl. 1-7.
- 1892a. Les formicides. Appendice III. In Grandidier, A., Hist. phys. nat. polit. Madagascar 20(2):229-280.
- 1892b. Nouvelles espèces de formicides de Madagascar (récoltées par M. Sikora). Ann. Soc. Entomol. Belg. 36:516-536.
1893. Nouvelles fourmis d'Australie et des Canaries. Ann. Soc. Entomol. Belg. 37:454-466.
1894. Abessinische und andere afrikanische Ameisen ... Mitt. Schweiz. Entomol. Ges. 9:64-100.
- 1895a. Nouvelles fourmis de diverses provenances, surtout d'Australie. Ann. Soc. Entomol. Belg. 39:41-49.
- 1895b. Nouvelles fourmis de l'Imerina Orientale (Moramanga, etc.). Ann. Soc. Entomol. Belg. 39:243-251.
- 1895c. Nouvelles fourmis d'Australie, récoltées a The Ridge, Mackay, Queensland par M. Gilbert Turner. Ann. Soc. Entomol. Belg. 39:417-428.
1899. Formicidae. Biol. Centr.-Amer. Hym. 3: 1-160.
- 1900a. Ponerinae et Dorylinae d'Australie, récoltées par MM. Turner, Froggatt, Nugent, Chase, Rothney, J.-J. Walker, etc. Ann. Soc. Entomol. Belg. 44:54-77.
- 1900b. Les formicides de l'Empire des Indes et de Ceylan. Part VII. J. Bombay Natur. Hist. Soc. 13:303-332.
1901. Nouvelles espèces de Ponerinae (avec un nouveau sous-genre et une espèce nouvelle d'Eciton). Rev. Suisse Zool. 9:326-353.
1902. Fourmis nouvelles d'Australie. Rev. Suisse Zool. 10:405-548.
1904. Fourmis du Musée de Bruxelles. Ann. Soc. Entomol. Belg. 48:168-177.
- 1905a. Miscellanea myrmecologiques II (1905). Ann. Soc. Entomol. Belg. 49:155-185.
- 1905b. Ameisen aus Java. Gesammelt von Prof. Karl Kraepelin 1904. Mitt. Natur. Hist. Mus., Hamburg, 22:1-26.
- 1907a. Formicides du Musée National Hongrois. Ann. Mus. Natl. Hungar. 5:1-42.
- 1907b. Ameisen von Madagaskar, den Comoren und Ostafrika. In Reise in Ostafrika in den Jahren 1903-1905 (A. Voeltzkow, ed.) 2(2):75-92. E. Schweizerbartsche Verlagsb., Stuttgart.
- 1907c. Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905 herausgegeben von Prof. W. Michaelson und Dr. R. Hartmeyer. 1:261-310. Jena, Verlag Gustav Fischer.
1908. Ameisen aus São Paulo (Brasilien), Paraguay etc., (gesammelt von Prof. Herm. von Jhering, Dr. Lutz, Dr. Fiebrig etc.). Verh. Zool.-bot. Ges. Wien. 58:340-418.
- 1909a. Fourmis du Musée de Bruxelles, fourmis de



- Benguela, récoltées par M. Creighton-Wellman, et fourmis du Congo, récoltées par MM. Lujá, Kohl, et Laurent. Ann. Soc. Entomol. Belg. 53:51-73.
- 1909b. Ameisen aus Guatemala usw., Paraguay und Argentinien. Deutsch. Ent. Zeitschr., pp. 239-269.
- 1910a. Formicidae australiens recus de MM. Froggatt et Rowland Turner. Rev. Suisse Zool. 18: 1-94.
- 1910b. Glanures myrmécologiques. Ann. Soc. Entomol. Belg. 54:6-32.
- 1910c. Fourmis des Philippines. Philippine J. Sci. 5:121-130.
- 1910d. Formicidae. In Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika, ausgeführt in den Jahren 1903-1905 (L. Schultze, ed.) 4:1-30, pl. 1. Jena, G. Fischer Verlag.
- 1910e. Note sur quelques fourmis d'Afrique. Ann. Soc. Entomol. Belg. 54:421-458.
- 1910f. Ameisen aus der Kolonie Erythräa, gesammelt von Prof. Dr. K. Escherich (nebst einigen in West-Abyssien von Herrn A. Ilg gesammelten Ameisen). Zool. Jahrb., Syst. 29:243-274.
- 1911a. Ameisen aus Ceylon, gesammelt von Prof. K. Escherich (einige von Prof. E. Bugnion). In Termitenleben auf Ceylon (K. Escherich, ed.), pp. 213-228. Jena, Verlag Gustav Fischer.
- 1911b. Fourmis nouvelles ou intéressantes. Bul. Soc. Vaud. Sci. Natur. 47:331-400.
- 1912a. Ameisen aus Java beobachtet und gesammelt von Edward Jacobson. Notes Leyden Mus. 34:97-112.
- 1912b. Fourmis des Seychelles et des Aldabras, reçues de M. Hugh Scott. Trans. Linn. Soc. London (2)15:159-167.
- 1913a. Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien. . . . II. Ameisen aus Sumatra, Java, Malacca und Ceylon, gesammelt von Herrn. Prof. Dr. v. Buttel-Reepen in den Jahren 1911-1912. Zool. Jahrb., Syst. 36:1-148.
- 1913b. Fourmis de Tasmanie et d'Australie récoltées par MM. Lea, Froggatt, etc. Bul. Soc. Vaud. Sci. Natur. 49:173-196, pl. 2.
- 1913c. H. Sauter's Formosa-Ausbeute: Formicidae II. Arch. Naturg. (A)79:183-202.
- 1913d. Ameisen aus Rhodesia, Kapland usw. . . . Deutsch. Entomol. Zeitschr., Beiheft, pp. 203-225.
- 1913e. Fourmis de Rhodesia, etc., récoltées par M. G. Arnold, le Dr. H. Brauns et K. Fikendey. Ann. Soc. Entomol. Belg. 57: 108-147.
- 1913f. Formicidae du Congo Belge, récoltées par MM. Bequaert, Lujá, etc. Rev. Zool. Afr. 2:306-351.
1914. Formicidae d'Afrique et d'Amerique nouveaux ou peu connus. Bul. Soc. Vaud. Sci. Natur. 50: 211-288.
1915. Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910-1913. 2. Ameisen. Ark. Zool. 9(16):1-119, pl. 1-3.
1916. Fourmis du Congo det d'autres provenances récoltées par MM. Hermann Kohl, Lujá, Mayné, etc. Rev. Suisse Zool. 24:397-460.
1922. Glanures myrmécologiques en 1922. Rev. Suisse Zool. 30:87-102.
- Gerstaecker, A.  
1859. Diagnosen der von Peters in Mossambique gesammelten Käfer und Hymenoptera, Schluss der Diagnosen der. . . Hymenopteren. Monatsber. k. Akad. Wiss. Berlin, 1858, pp. 261-264.
- Gotwald, W. H., Jr.  
1969. Comparative morphological studies of the ants, with particular reference to the mouthparts. Cornell Univ. Agr. Exp. Sta. Mem. 408:1-150.
- Karawajew, W.  
1925. Ponerinen (Fam. Formicidae) aus dem Indo-Australischen Gebiet. Konowia 4:69-81, 115-131, 276-296.
- Kempf, W. W.  
1964a. Uma nova *Platythyrea* do Brasil. Rev. Brasil. Entomol. 11:141-144.  
1964b. A propósito de um estudo sobre as formigas do gênero *Acanthostichus* Mayr. Pap. Avuls. Zool. S. Paulo 16:263-266.  
1972. Catálogo abreviado das formigas da região neotropical. Stud. Entomol. (n.s.) 15:3-344.
- Kusnezov, N.  
1959. La posición sistematica del genero *Metapone* Forel (Hymenoptera, Formicidae). Acta Zool. Lilloana 17:119-126.  
1962. El género *Acanthostichus* Mayr. Acta Zool. Lilloana 18:121-138.
- Mann, W. M.  
1916. The Stanford Expedition to Brazil, 1911, John C. Branner, director. The ants of Brazil. Bul. Mus. Comp. Zool. Harv. 60:399-490, pl. 1-7.  
1919. The ants of the British Solomon Islands. Bul. Mus. Comp. Zool. Harv. 63:275-391, pl. 1, 2.  
1921. The ants of the Fiji Islands. Bul. Mus. Comp. Zool. Harv. 69:399-499.  
1922. Ants from Honduras and Guatemala. Proc. U.S. Natl. Mus. 61(13):1-54.  
1923. Two new ants from Bolivia. Psyche 30:13-18.  
1931. A new ant from Porto Rico. J. Wash. Acad. Sci. 21:440-441.
- Mayr, G.  
1866. Diagnosen neuer und wenig gekannter Formiciden. Verh. Zool.-bot. Ges. Wien 16:885-908, pl. 20.

1870. Neue Formiciden. Verh. Zool.-bot. Ges. Wien 20:939-996.
  1878. Beiträge zur Ameisen-Fauna Asiens. Verh. Zool.-bot. Ges. Wien. 28:645-686.
  1887. Südamerikanische Formiciden. Verh. Zool.-bot. Ges. Wien, 37:509-632.
  1897. Formiciden aus Ceylon und Singapur. Termész. Fü. 20:420-436.
- Menozi, C.
- 1926- (1925). Nuove formiche della isole Filippine e di Singapore. Att. Soc. Sci. Natur. Mat. Modena 6:92-103.
  1931. Qualche nuova formiche di Costa Rica. Stettin. Entomol. Zeitg. 92:188-202.
  1932. Formiche dell'Isola di Nias. Misc. Zool. Sumatr., Medan, 65:1-13.
  1942. Formiche dell'Isola Fernando Po e del territorio del Rio Muni (Guinea Spagnola). Zool. Anz. 140:164-182.
- Motschulsky, V. de
1863. Essai d'un catalogue des insectes de l'île Ceylan (part). Bul. Soc. Impér. Natr. Moscou 36(3):1-153.
- Pate, V. S. L.
1947. A conspectus of the Tiphidae, with particular reference to the nearctic forms (Hymenoptera, Aculeata). J. N. Y. Entomol. Soc. 55:115-145.
- Rettenmeyer, C. W.
1963. Behavioral studies of army ants. Univ. Kansas. Sci. Bul. 44:281-465.
- Roger, J.
1860. Die Ponerä-artigen Ameisen. I. Berlin. Entomol. Zeitschr. 4:278-312.
  1861. Die Ponerä-artigen Ameisen (Schluss). Berlin. Entomol. Zeitschr. 5:1-54.
  1862. Einige neue exotische Ameisen-Gattungen und Arten. Berlin. Entomol. Zeitschr. 6:233-262.
- Santschi, F.
1910. Nouvelles fourmis de Tunisie (suite). Bul. Soc. Hist. Natur. Afr. Nord 2:70-72.
  1911. Nouvelles fourmis du Congo et du Benguela. Rev. Zool. Afr. 1:204-217.
  1912. Fourmis d'Afrique et de Madagascar. Ann. Soc. Entomol. Belg. 56:150-167.
  1913. Mélanges myrmécologiques. Ann. Soc. Entomol. Belg. 57:429-437.
  - 1914a. Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912). Résultats scientifiques. Insectes Hyménoptères. II. Formicidae, pp. 41-148, pl. 1-3. Paris, Libr. A. Schulz.
  - 1914b. Formicides de l'Afrique occidentale et australe. Bul. Lab. Zool. Gen. Agr., Portici, 8:307-385.
  1915. Nouvelles fourmis d'Afrique. Ann. Soc. Entomol. France 84:244-282.
  1921. Ponerinae, Dorylinae et quelques autres formicides neotropiques. Bul. Soc. Vaud. Sci. Natur. 54:81-103.
1923. Descriptions de nouveaux Formicides éthiopiens et notes diverses.—I. Rev. Zool. Afr. 11:259-295.
1924. Nouvelles fourmis brésiliennes. Ann. Soc. Entomol. Belg. 64:5-20.
1928. Formicidae. Insects of Samoa 5:41-58.
1930. Description de formicides éthiopiens nouveaux ou peu connus. V. Bul. Ann. Soc. Entomol. Belg. 70:49-77.
1932. Quelques fourmis inédites de l'Amérique centrale et Cuba. Rev. Ent., Rio de Jan. 2:410-414.
1933. Fourmis de la République Argentine, en particulier du territoire de Misiones. An. Soc. Cienc. Argent. 116:105-124.
1934. Fourmis de Misiones et du Chaco Argentin. Rev. Soc. Entomol. Argent. 6:23-34.
1937. Fourmis du Congo et régions limitrophes. Rev. Zool. Bot. Afr. 30:71-85.
- Schneirla, T. C.
1949. Army-ant life and behavior under dry-season conditions. 3. The course of reproduction and colony behavior. Bul. Amer. Mus. Natur. Hist. 94:1-82.
  1971. Army ants. In A study in social organization (H. R. Topoff, ed.). W. H. Freeman and Co., San Francisco. xxi + 349 pp.
- Smith, F.
1857. Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mt. Ophir, Malacca; and at Singapore by A. R. Wallace. J. Proc. Linn. Soc. London 2:42-130.
  1858. Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. London, 216 pp., 14 pl.
  1859. Catalogue of hymenopterous insects collected by Wallace at the islands of Aru and Key. J. Proc. Linn. Soc. London, Zool. 3:132-178.
- Smith, M. R.
1942. The males of two North American cerapachyine ants. Proc. Entomol. Soc. Wash. 44:62-64.
  1947. A generic and subgeneric synopsis of the United States ants, based on the workers (Hymenoptera: Formicidae). Amer. Midl. Naturalist 37:521-647.
  1949. A new species of *Probolomyrmex* from Barro Colorado Island, Canal Zone. Proc. Entomol. Soc. Wash. 51:38-40.
  1955. *Acanthostichus* (*Ctenopyga*) *townsendi* (Ashm.), a synonym of *Acanthostichus texanus* Forel (Hymenoptera: Formicidae). Bul. Brooklyn Entomol. Soc. 50:48-50.
- Spinola, M.
1853. Compte-rendu des Hyménoptères inédits provenant du voyage entomologique de M. Ghiliani

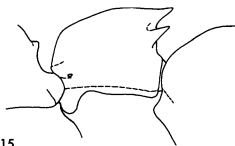
- dans le Para en 1846. *Mem. R. Acad. Sci. Torino* (2)13:19-94.
- Stütz, H.  
1932. Formicidae. In: Norwegian zoological expedition to the Galapagos Islands, 1925, conducted by Alf Wollebaek. *Meddel. Zool. Mus. Oslo* 31: 367-372.
- Taylor, R. W.  
1965a. New Melanesian ants of the genera Simopone and Amblyopone (Hymenoptera-Formicidae) of zoogeographic significance. *Brev. Mus. Comp. Zool. Harv.* 221:1-11.  
1965b. A monographic revision of the rare tropicopolitan ant genus *Probolomyrmex* Mayr. *Trans. R. Entomol. Soc. London* 117:345-365.  
1966- Notes on the Indo-Australian ants of genus (1965). *Simopone* Forel (Hymenoptera-Formicidae). *Psyche* 72:287-290.
- Viehmeyer, H.  
1913. Ameisen aus dem Kopal von Celebes. *Stettiner Entomol. Z.*, pp. 141-155.  
1916a. Ameisen von Singapore beobachtet und gesammelt von H. Overbeck. *Arch. Natrg. (A)*81: 108-168.  
1916b. Ameisen von Philippinen und anderer Herkunft (Hym.). *Entomol. Mitt.* 5:283-291.  
1924. Formiciden der australischen Faunenregion. *Entomol. Mitt.* 13:219-229, 310-319.
- Weber, N. A.  
1939. New ants of rare genera and a new genus of ponerine ants. *Ann. Entomol. Soc. Amer.* 32: 91-104.  
1940. Rare ponerine genera in Panama and British Guiana. *Psyche* 47:75-84.  
1942. New doryline, cerapachyine, and ponerine ants from the Imatong Mountains, Anglo-Egyptian Sudan. *Proc. Entomol. Soc. Wash.* 44:40-49.  
1949. New African ants of the genera *Cerapachys*, *Phryacaces*, and *Simopone*. *Amer. Mus. Novit.* 1396:1-9.
- Wheeler, G. C.  
1950. Ant larvae of the subfamily Cerapachyinae. *Psyche* 57:102-113.
- Wheeler, G. C., and Wheeler, J.  
1952. The ant larvae of the subfamily Ponerinae. *Amer. Midl. Naturalist* 48:111-144, 604-672.  
1964a. The ant larvae of the subfamily Cerapachyinae: Supplement. *Proc. Entomol. Soc. Wash.* 66: 65-71.  
1964b. The ant larvae of the subfamily Ponerinae: Supplement. *Ann. Entomol. Soc. Amer.* 57: 443-462.  
1971. Ant larvae of the subfamily Ponerinae: Second supplement. *Ann. Entomol. Soc. Amer.* 64: 1197-1217.
1974. Supplementary studies on ant larvae: Cerapachyinae, Pseudomyrmecinae, and Myrmicinae. *Psyche* 80:204-211.
1974. Supplementary studies on ant larvae: Simopone and Turneria. *J. New York Entomol. Soc.* 82:103-105.
- Wheeler, W. M.  
1902. An American Cerapachys, with remarks on the affinities of the Cerapachyinae. *Biol. Bul.* 3: 181-191.  
1903. Some notes on the habits of *Cerapachys augustae*. *Psyche* 10:205-209.  
1909. Ants collected by Prof. F. Silvestri in the Hawaiian Islands. *Bol. Lab. Zool. Gen. Agr., Portici*, 3:269-272.  
1910. Ants, their structure, development and behavior. Columbia University Press, New York. xxv + 663 pp.  
1914. The ants of the Baltic Amber. *Schrift. Phys.-ökon. Ges. Königsberg* 55:1-142.  
1918. The Australian ants of the ponerine tribe Cerapachyini. *Proc. Amer. Acad. Arts Sci.* 53:215-265.  
1919. The ants of Borneo. *Bul. Mus. Comp. Zool. Harv.* 63:43-147.  
1920. The subfamilies of Formicidae, and other taxonomic notes. *Psyche* 27:46-55.  
1922a. The ants collected by the American Museum Congo Expedition. *Bul. Amer. Mus. Natur. Hist.* 45:39-269, pl. 2-23.  
1922b. Keys to the genera and subgenera of ants. *Bul. Amer. Mus. Natur. Hist.* 45:631-710.  
1922c. A synonymic list of the ants of the Ethiopian region. *Bul. Amer. Mus. Natur. Hist.* 45:711-1004.  
1922d. A synonymic list of the ants of the Malagasy region. *Bul. Amer. Mus. Natur. Hist.* 45:1005-1055.  
1924a. The Formicidae of the Harrison Williams Galapagos Expedition. *Zoologica*, New York, 5: 101-122.  
1924b. On the ant-genus *Chrysapace* Crawley. *Psyche* 31:224-225.  
1928. Ants collected by Professor F. Silvestri in China. *Bol. Lab. Zool. Gen. Agr., Portici*, 22:3-38.  
1929. Ants collected by Professor F. Silvestri in Formosa, the Malay Peninsula and the Philippines. *Bol. Lab. Zool. Gen. Agr., Portici*, 24:27-64.  
1934. Neotropical ants collected by Dr. Elisabeth Skwarra and others. *Bul. Mus. Comp. Zool. Harv.* 77:157-240.  
1937. Ants mostly from the mountains of Cuba. *Bul. Mus. Comp. Zool. Harv.* 81:441-465.
- Wheeler, W. M., and Chapman, J. W.  
1925. The ants of the Philippine Islands. Part I. Dory-

- linae and Ponerinae. Philippine J. Sci. 28: 49-73, pl. 1, 2.
- Wheeler, W. M., and Mann, W. M.  
1914. The ants of Haiti. Bul. Amer. Mus. Natur. Hist. 33:1-61.
- Wilson, E. O.  
1957. The discovery of cerapachyine ants on New Caledonia, with descriptions of new species of Phyracaces and Sphinctomyrmex. Brev. Mus. Comp. Zool. Harv. 74:1-9.  
1958a. The beginnings of nomadic and group-predatory behavior in the ponerine ants. Evolution 12: 24-31.  
1958b. Studies on the ant fauna of Melanesia. I. The tribe Leptogenyini. II. The tribes Amblyoponini and Platythyreini. Bul. Mus. Comp. Zool. Harv. 118:101-153.  
1958c. Observations on the behavior of the cerapachyine ants. Insectes Sociaux 5:129-140.  
1959. Studies on the ant fauna of Melanesia. VI. The tribe Cerapachyini. Pacific Insects 1:39-57.
- Wilson, E. O., and Regnier, F. E., Jr.  
1971. The evolution of the alarm-defense system in the formicine ants. Amer. Naturalist 105:279-289.
- Wilson, E. O., and Taylor, R. W.  
1967. The ants of Polynesia (Hymenoptera: Formicidae). Pacific Insects Monogr. 14:1-109.

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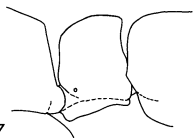
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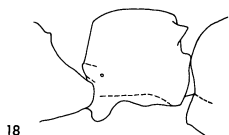
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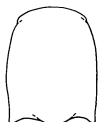
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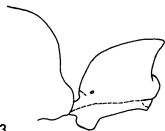
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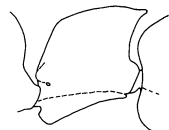
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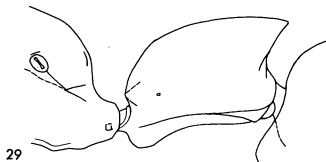
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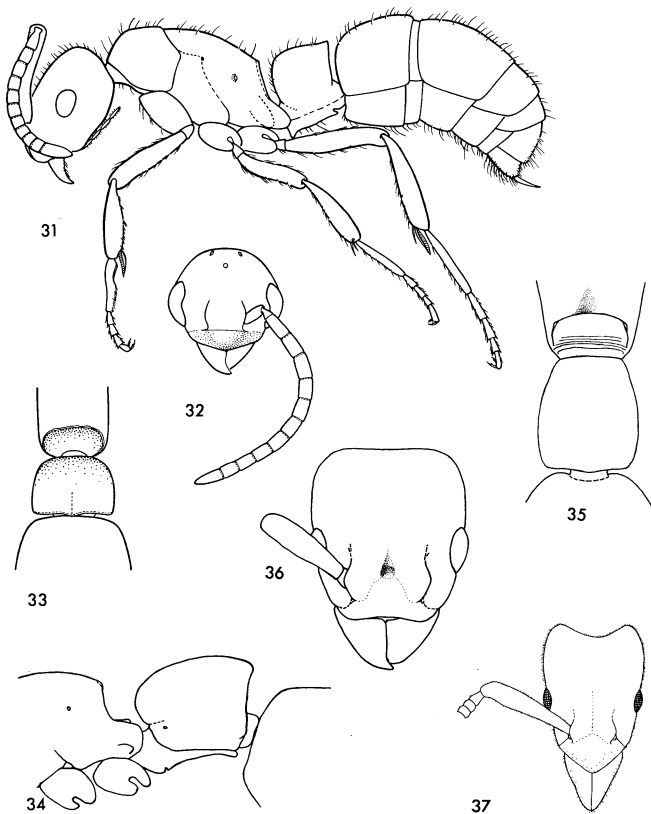
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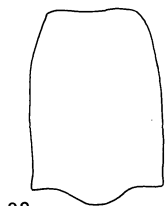
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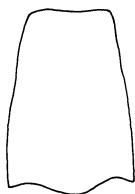


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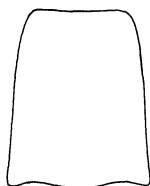
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*P. pilosula*



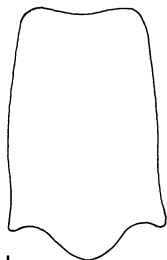
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*P. angusta*



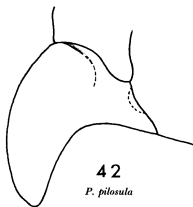
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*P. punctata*



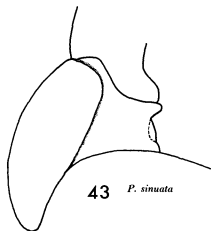
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*P. sinuata*



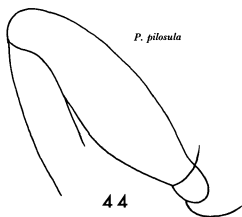
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*P. pilosula*



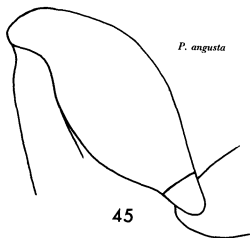
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*P. sinuata*



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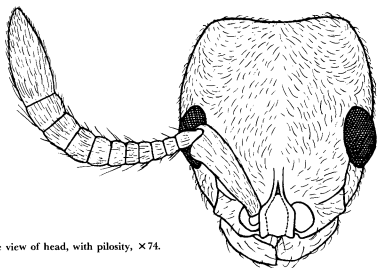
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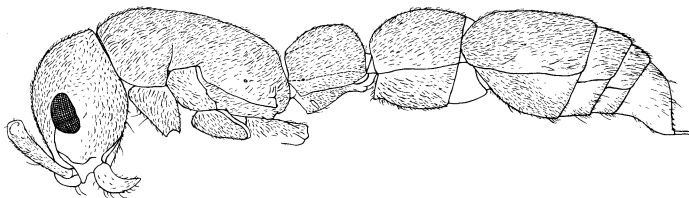
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*P. angusta*

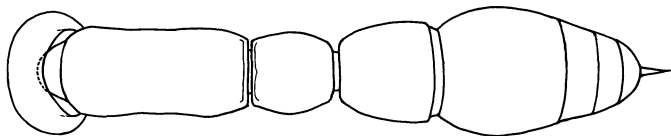
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51. Full-face view of head, with pilosity,  $\times 74$ .



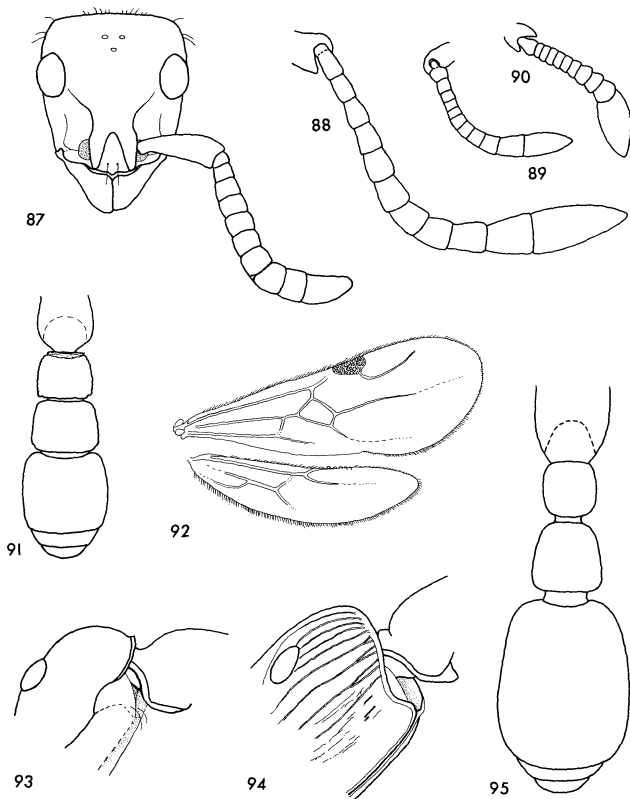
52. Side view of body, with pilosity,  $\times 47$ .



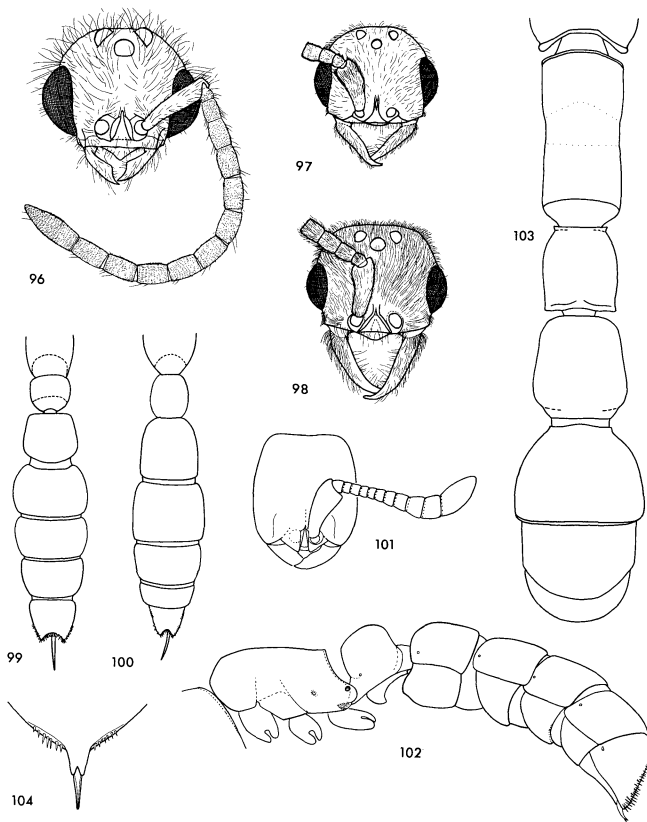
53. Dorsal-view outline of body, pilosity omitted,  $\times 47$ .

Figures 51–53. *Cerapachys pruinosus* n. sp., holotype worker from Negros I., Philippines.



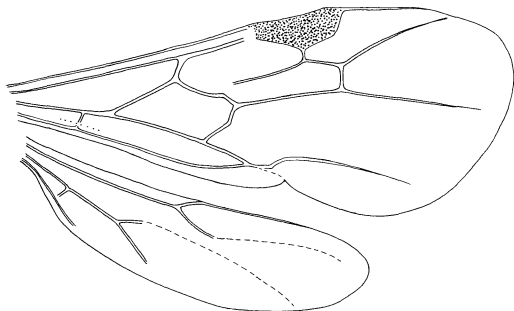


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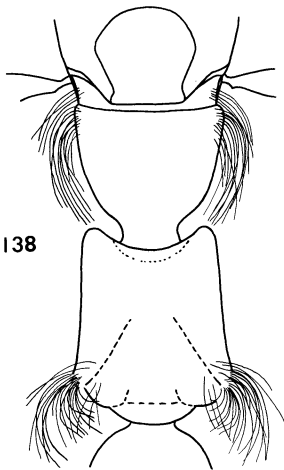


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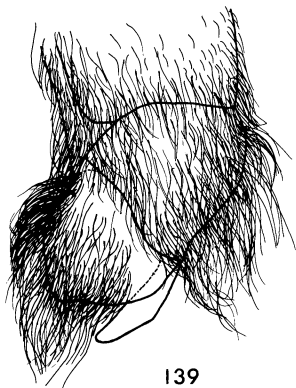
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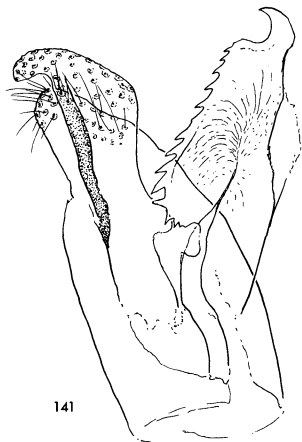
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